Title: **Ecological traits modulate bird species responses to forest fragmentation in an Amazonian anthropogenic archipelago**

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ABSTRACT

Aim We assessed patterns of avian species loss and the role of ecological traits in explaining species vulnerability to forest fragmentation in an anthropogenic island system. We also contrasted observed and detectability-corrected estimates of island occupancy, which are often used to infer species vulnerability.

Location Tucuruí Hydroelectric Reservoir, eastern Brazilian Amazonia.

Methods We surveyed forest birds within 36 islands (3.4–2551.5 ha) after 22 years of isolation history. We applied species-area relationships to assess differential patterns of species loss among three datasets: all species, forest specialists, and habitat generalists. After controlling for phylogenetic non-independence, we used observed and detectability-corrected estimates of island occupancy separately to build competing models as a function of species traits. The magnitude of the difference between these estimates of island occupancy was contrasted against species detectability.

Results The rate of species loss as a function of island area reduction was higher for forest specialists than for habitat generalists. Accounting for the area effect, forest fragmentation did not affect the overall number of species regardless of the dataset. Only the interactive model including natural abundance, habitat breadth, and geographic range size was strongly supported for both estimates of island occupancy. For 30 species with detection probabilities below 30%, detectability-corrected estimates were at least ten-fold higher than those observed. Conversely, differences between estimates were negligible or non-existent for all 31 species with detection probabilities exceeding 45.5%.

Main conclusions Predicted decay of avian species richness induced by forest loss is affected by the degree of habitat specialisation of the species under consideration, and may be unrelated to forest fragmentation *per se*. Natural abundance was the main predictor of species island occupancy, although habitat breadth and geographic range size also played a role. We caution against using occupancy models for low-detectability species, because overestimates of island occupancy reduce the power of species-level predictions of vulnerability.

INTRODUCTION

Amazonian forests have been extensively converted to cattle pastures and cropland inducing widespread loss and fragmentation of formerly continuous forests, especially in the eastern and southern portions of the basin (Laurance et al., 2001; Peres et al., 2010). This scenario is further exacerbated by a massive growth in hydroelectric dams, which invariably inundate large tracts of forest, creating archipelagic landscapes (Lees et al., 2016). Forest fragmentation is widely recognised as a pervasive and lasting threat to biodiversity and ecosystem functioning since forest fragments are subject to the combined detrimental effects of core area reduction, edge proliferation, and isolation (Haddad et al., 2015). Nevertheless, the quality of the matrix surrounding forest fragments plays a major role in determining the severity of fragmentation (Kennedy et al., 2010). Old-growth forest fragments surrounded by secondary forests favour several species that exploit matrix resources (Blake & Loiselle, 2001), are less affected by edge effects (Laurance et al., 2011), and are more permeable, ensuring species movements among forest fragments (Powell et al., 2013). Conversely, forest islands within hydroelectric reservoirs exhibit lower functional connectivity, are expected to be dominated by edge-mediated decay in forest structure (Benchimol & Peres, 2015), and harbour depauperate extinction-driven species assemblages (Wolfe et al., 2015). The detrimental consequences of forest fragmentation are therefore amplified by a water matrix (Mendenhall et al., 2014), rendering hydroelectric dams a more severe threat to forest biotas.

Habitat loss and fragmentation are the twin processes associated with land-use change. From a species perspective, the former is defined as the conversion of a 'habitat' into a 'non-habitat' (i.e. habitat amount shrinkage), and the latter as the subdivision of a single large 'habitat' into several smaller 'habitat patches' separated from one another by an intervening 'non-habitat' matrix (Lindenmayer & Fischer, 2007). While habitat loss has pervasive detrimental effects on native biodiversity, fragmentation affects species differently (Fahrig, 2003). For instance, habitat specialists are more consistently impaired by fragmentation than habitat generalists (Devictor et al., 2008). Predictions of species loss based on species-area relationships are therefore expected to be underestimated for habitat specialists if habitat generalists are included in the species pool (Matthews et al., 2014). Moreover, habitat fragmentation *per se* (i.e. accounting for habitat loss) may either decrease or increase the number of species that would be predicted by habitat loss alone (Yaacobi et al., 2007). Therefore, a proper assessment of species loss in variable-sized habitat patches

should focus on groups of target species (Matthews et al., 2014) and disentangle the effects of habitat loss from fragmentation (Fahrig, 2003; Yaacobi et al., 2007).

Species-level studies on responses to habitat fragmentation can further enhance our understanding of vulnerability-prone traits at both landscape (Feeley et al., 2007) and global scales (Bregman et al., 2014), complementing assemblage-wide studies (Moura et al., 2016). Accordingly, low-density, large-bodied species at high trophic levels (Ewers & Didham, 2006), and those with restrict habitat breadth (Henle et al., 2004) and wide geographic range (Newbold et al., 2014) are expected to be at higher risk of extinction. The same holds true for bird species inhabiting the lower strata of closed-canopy forests (Sekercioglu et al., 2002), following ant-swarms and foraging in mixed-species flocks (Stouffer & Bierregaard, 1995). Understanding trait-based patterns of extinction proneness is therefore invaluable to anticipate species losses and tailor conservation programs to vulnerable species. However, idiosyncratic species responses across different regions (Gage et al., 2004; Moura et al., 2016), and the co-occurrence of confounding factors in human-modified landscapes, such as matrix type, may limit the extent to which clear patterns can be uncovered (Ewers & Didham, 2006), reinforcing the need for landscape-scale studies.

In fragmented landscapes, the area of remaining patches is the main driver of species patch occupancy (Keinath et al., 2017). Area-sensitive species can no longer occur in patches below a minimum spatial requirement, and are consequently relegated to fewer patches than species requiring smaller areas (Dardanelli et al., 2006). Thus, the proportion of patches occupied in a landscape has often been used as a measure of species vulnerability to habitat fragmentation (e.g. Meyer et al., 2008; Thornton et al., 2011; Wang et al., 2015). Due to inherent differences in species detectability and the fact that non-detections do not necessarily imply absences, observed estimates of patch occupancy can be underestimated. To overcome this bias, occupancy modelling has often been uncritically used as it can estimate patch occupancy while accounting for imperfect detectability (Banks-Leite et al., 2014). Unlike observed estimates, this analytical approach can overestimate patch occupancy for species with low detection probability (< 30%; MacKenzie et al., 2002), which may degrade inferential power about species vulnerability.

Habitat fragmentation research has largely focused on terrestrial landscapes (Fahrig, 2017), where the remaining habitat (i.e. area of native vegetation) is typically termed as ‘remnant’, ‘fragment’, or ‘patch’. Nonetheless, the term ‘island’ best describes remaining

habitats in archipelagic landscapes. To avoid misleading terminology (Hall et al., 1997), herein we refer to the remaining habitats in terrestrial and archipelagic landscapes as 'fragments' and 'islands', respectively. Meanwhile, the term 'patch' is used to encompass both 'fragment' and 'island'. In this study, we assessed bird species responses to forest fragmentation in a vast archipelagic landscape induced by a major hydroelectric dam in eastern Brazilian Amazonia, while addressing the four following questions. First, do habitat generalists show a less steep decline in species richness as a function of island area reduction compared to forest specialists? If so, we predict that assessments of overall species loss relying on species-area relationships also underestimate the loss of forest specialists in reservoir islands as previously shown for forest fragments (Matthews et al., 2014). Second, does forest fragmentation *per se* exacerbate or reduce the impact of forest loss on species richness for the overall species pool, forest specialists, and habitat generalists? We predict a neutral fragmentation effect on the overall species pool due to a negative effect on forest specialists and a positive effect on habitat generalists. Third, which suite of morpho-ecological traits best explains species rates of island occupancy within the forest archipelago? This allowed us to determine which species are most or least prone to extirpation from anthropogenic island systems to anticipate species losses driven by existing and future hydroelectric impoundments in lowland tropical forests. Fourth, how divergent are observed and detectability-corrected estimates of island occupancy for rarely detected species? We show distinct responses to forest loss between forest specialists and habitat generalists, and that forest fragmentation *per se* may not affect the overall number of species in forest islands. We also emphasize the use of rarity metrics to assess species vulnerability to forest fragmentation, and caution against the use of occupancy models to infer island occupancy rates when species detection probability is low.

METHODS

Study area

This study was carried out within the vast Tucuruí Hydroelectric Reservoir (hereafter, THR; 4°16' S, 49°34' W), located in the State of Pará, eastern Brazilian Amazonia (Fig. 1). The reservoir was formed in 1984 when the Tocantins River was dammed, flooding over 250,000 ha of pristine lowland forests and creating some 2,200 islands on higher elevation terrain. In 2002, the entire archipelago and surrounding areas were set aside as a sustainable-use reserve

(IUCN category VI), spanning 568,667 ha. This protected area – Tucuruí Lake Environmental Protection Area (APA Lago de Tucuruí, in Portuguese) – is a multiple-use mosaic designated to meet both the interests of local communities and wildlife conservation.

The vegetation is typical of Amazonian *terra firme* forests, containing 80–90% forest cover and an understorey dominated by several palm species (Ferreira et al., 2012). The climate is tropical monsoon, with a rainy season from December to May and a dry season from June to November (Alvares et al., 2013). Mean annual precipitation and temperature are 2,354 mm and 27.5 ºC, respectively (Alvares et al., 2013).

The THR is located in the most deforested region of Brazilian Amazonia, known as the 'Arc of Deforestation', and encompasses both the Xingú and Belém lowland areas of endemism, which are separated by the Tocantins River (Silva et al., 2005). To survey the forest avifauna of the reservoir, we selected an even number of islands across a comparable size range on each bank of the former river channel. Many islands and mainland sites surrounding the reservoir were heavily degraded, but we surveyed a set of 36 relatively undisturbed forest islands located within (n = 26) or adjacent to (n = 10) the two Wildlife Protection Zones (ZPVS): ZPVS 3 on the left bank and ZPVS 4 on the right bank (Fig. 1b). The two largest islands (> 1,800 ha) were defined as 'pseudo-controls', and 34 smaller islands as 'treatments', which were selected to maximise the range of island sizes, shapes and degrees of connectivity (see Table S1 in Supporting Information). The pseudo-control island on the right bank is actually a mainland peninsula that was semi-isolated along a boundary of secondary forest.

Avian surveys

We conducted six field campaigns over a 15-month period: 6–25 August and 12–29 November in 2006, and 4–22 March, 12 April–1 May, 14–31 July and 22 September–10 October in 2007. During each field campaign, all 36 islands were surveyed once using 10-min point counts by experienced observers (S.M.D. or L.M.P.H.) accompanied by a field assistant, who simultaneously recorded bird vocal activity (using a Sony TCM-5000 recorder and a semi-directional microphone) as a voucher of species occurrences. To ensure that all birds recorded were within surveyed islands, we restricted all individuals seen or heard to within an estimated 50-m radius from the observer and discarded all flyovers. Given our focus on diurnal forest species, we also discarded all aquatic, nocturnal and aerial species, as

well as every species that 'does not normally occur in forest' (*sensu* BirdLife International, 2017). Surveys were usually carried out between 06:00 and 10:00 h avoiding rainy and windy weather. The number of point count stations (hereafter, PCs) surveyed per island, which ranged between 2 and 33 (see Table S1), was roughly proportional to island area on a log-log scale (r^2_{adj} = 0.863, P < 0.001). All 36 islands were surveyed along linear transects – three of each placed at the two pseudo-control islands and one at each of the 34 treatment islands – along which PCs were distributed at regular 200-m intervals. A total of 240 PCs was visited six times each, amounting to 1,388 samples.

Sampling sufficiency per island was represented by individual-based rarefaction curves produced with 1,000 bootstrap replications in the *iNEXT* R package (Hsieh et al., 2016; R Core Team, 2016). Sampling completeness per island was quantified as a percentage between the recorded and the estimated number of species based on the first-order Jackknife estimator (Willie et al., 2012) calculated using the *vegan* package (Oksanen et al., 2017).

Species traits

We classified the degree of habitat specialisation of each species into 'forest specialist' or 'habitat generalist' based on two attributes extracted from BirdLife International (2017), namely 'forest dependency' and 'habitats'. Species had to meet two criteria to be classified as forest specialists: (i) 'high' forest dependency and (ii) 'Forest – Subtropical/Tropical Moist Lowland'– the equivalent to Amazonian lowland forest – listed as a habitat of 'major' importance. Species that did not meet these criteria were classified as habitat generalists. Accordingly, a habitat generalist is a species that occurs in forest (i.e. 'low', 'medium' or 'high' forest dependency) but does not have 'Forest – Subtropical/Tropical Moist Lowland' listed as a habitat of 'major' importance. For example, *Pitangus sulphuratus* has a 'low' forest dependency and occurs throughout nine habitat types, including 'Forest – Subtropical/Tropical Moist Lowland' which is listed as a habitat of 'suitable' importance. Likewise, *Onychorhynchus coronatus* was classified as a habitat generalist, despite its 'high' forest dependency, because this species is mostly associated with riparian habitats (Bueno et al., 2012) and this habitat type (i.e. 'Forest – Subtropical/Tropical Swamp') was inundated by the THR floodwaters. Habitat generalist is then a species that may use the 'Forest – Subtropical/Tropical Moist Lowland' habitat as an alternative habitat. Habitat specialisation

was used to examine whether patterns of species loss differed between forest specialists and habitat generalists.

We also compiled data on seven additional traits associated with avian extinction risk (Sodhi et al., 2004): body mass, trophic level, vertical stratum, flocking behaviour, geographic range size, habitat breadth, and natural abundance (herein defined as the total number of individuals recorded within pseudo-control islands) (see Table S2 for variable descriptions and sources, and Table S3 for species traits). We $\log_{10}$-transformed body mass (g), geographic range size (km^2), and natural abundance ($n + 1$) prior to analysis. Trophic level is a continuous variable estimated from proportional consumption of food items across five diet categories. Vertical stratum and flocking behaviour were converted from nominal to ordinal (rank) variables to produce a gradient from ground to canopy strata, and from low to high levels of gregariousness, respectively. Stotz et al. (1996) classified 41 habitats for the Neotropical avifauna and assigned 1 to 7 habitats used by each species. Habitat breadth was then defined as a count variable representing the number of habitats used, with lower and higher values indicating restricted and broad habitat breadth, respectively. These traits were used to assess patterns of species occupancy across all 36 surveyed islands.

Island and landscape metrics

We used four RapidEye© imagery tiles (250,000 ha at 5-m resolution) covering all surveyed islands and an unsupervised classification performed in ESRI ArcMap 10.2 to produce a categorical map with two land-cover classes: island and water (Fig. 1c). We then extracted three spatial metrics for each island: island area in hectares (AREA), shape index (SHAPE), and proximity index (PROX). SHAPE is a measure of the deviation in the perimeter of a given island from the perimeter (m) of a perfect circle with the same area (m^2), and calculated as perimeter/$[2\sqrt{(\pi \times \text{area})}]$, with lower and higher values indicating simple and complex shapes, respectively (Burchell et al., 2012). PROX (*sensu* McGarigal et al., 2012) was used as a measure of connectivity, and considered the total area of any island ($\geq$ 1 ha) that was partially or entirely within a 500-m external buffer (Benchimol & Peres, 2015), with smaller values indicating lower connectivity or higher isolation. We arbitrarily assigned a PROX value one order of magnitude greater than the most connected island for pseudo-control islands, and a value of 0.01 for the least connected island. Finally, we $\log_{10}$-transformed both AREA and PROX prior to analysis.

246

247 **Species-area relationships and forest fragmentation effect**

248 The logarithmic form of the species-area relationship (type IV curve *sensu* Scheiner, 2003)
249 was used in order to allow us to fit simple linear regression models (hereafter, SAR models;
250 Rosenzweig, 1995) for three datasets – all species, only forest specialists, and only habitat
251 generalists – according to the following equation:

252 $$\log_{10}(S) = z \times \log_{10}(A) + \log_{10}(c)$$

253 where S = number of species, z = regression slope, A = island area (ha), c = regression
254 intercept. As forest specialists were not recorded at one small surveyed island, S was
255 standardised as $\log_{10}(n + 1)$. To test whether z-values for forest specialists and habitat
256 generalists were significantly different ($P \leq 0.05$), we performed an ANCOVA model with
257 habitat specialisation as the categorical independent variable.

258 We examined whether forest fragmentation *per se* either exacerbates or reduces
259 species loss as a function of forest loss (i.e. island area reduction), following Yaacobi et al.
260 (2007). Accordingly, after fitting SAR models for each dataset, we extrapolated the number
261 of species to a hypothetical island with the combined area of all 36 surveyed islands (6,502.6
262 ha). We then compared the overall number of species recorded across the whole set of
263 surveyed islands (i.e. gamma diversity) with the extrapolated number of species to the
264 hypothetical island (i.e. predicted alpha diversity) for each dataset. If the gamma diversity is
265 lower or higher than the predicted alpha diversity of the hypothetical island, forest
266 fragmentation will have either exacerbated or reduced species loss, respectively. In other
267 words, additional factors other than forest loss operate in explaining the gamma diversity,
268 which we attributed to forest fragmentation. Values were considered significantly different if
269 the overall number of species recorded was outside the 95% confidence interval of the
270 extrapolated number of species. Since the accuracy of this method relies on SAR model fits,
271 we deemed the method as appropriate if the z-value was significant and the r^2_{adj} was ≥ 0.5
272 (Matthews et al., 2016b).

273 Previous studies have shown that departures in the overall number of species recorded
274 from that predicted by extrapolating SAR models are related to the nested structure of species
275 assemblages (Santos et al., 2010; Matthews et al., 2016b). To examine how the degree of
276 nestedness relates to the fragmentation effect on species richness, we quantified the nested

structure of the three datasets using the nestedness metric based on overlap and decreasing fill (NODF) as this metric is statically robust to overestimating nestedness (i.e. type I statistical errors; Almeida-Neto et al., 2008). We used the NODF-Program, version 2.0 (Almeida-Neto & Ulrich, 2011), to calculate NODF values for all three datasets and for 1,000 simulated assemblages generated with the proportional-row and proportional-column (PP) null model algorithm (Ulrich & Gotelli, 2012). NODF Z-transformed scores (hereafter, Z-scores) were then used to determine whether the nested (positive Z-scores) or anti-nested (negative Z-scores) structure of species assemblages were significantly different from those of simulated assemblages (Matthews et al., 2015).

Species vulnerability to forest fragmentation

Species vulnerability to forest fragmentation corresponds to the risk of a species to become locally extinct across the whole set of forest patches remaining in the landscape. Hence, species occurring in a few patches would be more extinction-prone than those occurring in many patches, particularly if an extinction debt has yet to be paid and patch colonization rates are low, which is likely the case of forest archipelagos within hydroelectric reservoirs (Jones et al., 2016). In this case, patch occupancy is inversely related to vulnerability to forest fragmentation. However, species absences from a patch does not necessarily imply that local extinctions had occurred because such species could be initially absent from the patch at the time of its creation (Bolger et al., 1991), meaning that patch occupancy may not always indicate vulnerability to forest fragmentation (Keinath et al., 2017). Therefore, we first examined whether local extinction had actually occurred across surveyed islands by comparing the SARs for birds in very large pseudo-control islands with that in much smaller treatment islands (Brown, 1971; Bolger et al., 1991; Wang et al., 2009). To accomplish this, we used the number of bird species as a function of surveyed area (number of PCs × non-overlapping point count area), and performed an ANCOVA model with island type as the categorical independent variable (see Appendix S1 for further details). We found that the predicted line derived from treatment islands was well below and had a steeper slope than that of pseudo-control islands (see Fig. S2a), indicating that local extinctions had occurred in the former. Subsequently, we estimated the number of local extinctions that had occurred in each treatment island by subtracting the predicted number of species in pseudo-control islands from the recorded number of species in treatment islands (Bolger et al. 1991).

Accordingly, we estimated a total of 788 local extinctions across all 34 treatment islands over 22-23 years of post-isolation history at the THR landscape (see Fig. S2b). Given these results, we used estimates of island occupancy (i.e. proportion of islands occupied – PIO) as a measure of species vulnerability to forest fragmentation based on species occurrence across all 36 surveyed islands.

Due to potential biases introduced by imperfect detectability, we calculated both the observed and detectability-corrected PIO for each species (Thornton et al., 2011; Wang et al., 2015). The latter was calculated using single-season occupancy models (MacKenzie et al., 2002) implemented in the *unmarked* package (Fiske & Chandler, 2011). As some species can occasionally disperse across islands by traversing the water matrix and our bird surveys were conducted over six discrete field campaigns, we relaxed the closure assumption of single-season models, which is defensible as long as (i) changes in island occupancy status occur at random – which is likely the case – and (ii) 'occupancy' is interpreted as 'use' (Mackenzie & Royle, 2005).

We modelled species occupancy probability (ψ) as a function of island AREA, SHAPE, and PROX, assuming an interactive effect between AREA and SHAPE due to their combined effects in determining the severity of edge-effects. As sampling effort increases the chances of detecting any given species, we modelled the detection probability (p) as a function of the number of PCs per island (EFFORT). We also considered both ψ and p as constants across islands. Accordingly, we built 16 competitive occupancy models for each species (Table 1). We then used the Akaike information criterion (AIC) to rank models and to calculate Akaike weights to indicate the best fit models (Burnham & Anderson, 2002). From model-averaging based on all models with high support ($\Delta AIC \leq 2$), we summed the occupancy probability at each island and divided this by the total number of surveyed islands to obtain the detectability-corrected PIO for each species (Thornton et al., 2011; Wang et al., 2015). We also summed the detection probability for each visit per island and divided by 216 (36 islands × 6 surveys) to obtain the overall detection probability for each species.

Species traits and vulnerability to forest fragmentation

It is widely assumed that closely-related species share more traits than distantly-related species (Webb et al., 2002). Thus, analyses involving species as sampling units should be corrected for phylogenetic non-independence among traits (Freckleton et al., 2002). To

account for this, we built a majority-rule consensus tree based on 1,000 trees obtained from birdtree.org ('Hackett All Species'; Jetz et al., 2012) using the *ape* package (Paradis et al., 2004). As a consensus tree does not include branch lengths, we set all branch lengths equal to one. We then performed Phylogenetic Generalised Least Squares (PGLS) using the *caper* package (Orme et al., 2013) and Pagel's lambda branch length transformation optimised by maximum likelihood (Freckleton et al., 2002). We examined both observed and detectability-corrected PIO separately as response variables and species traits as explanatory variables.

To assess the role of ecological traits in explaining species vulnerability to forest fragmentation, we built 13 competing PGLS models including a univariate model for each of the seven traits, three additive models, and three interactive models. Additive and interactive models were built under the same combination of traits. The first included natural abundance, habitat breadth, and geographic range size, and is referred to as 'rarity model' as it combines all three dimensions of rarity (*sensu* Rabinowitz, 1981). The second included natural abundance, body mass, and trophic level, and is referred to as 'population size model', following Meyer et al. (2008). The third included trophic level, vertical stratum, and flocking behaviour, and is referred to as 'foraging model'.

RESULTS

Considering all 36 surveyed islands, we recorded 10,575 individuals representing 207 bird species, 150 genera, and 31 families. The number of individuals recorded per island ranged from 28 to 1,997 (mean ± SD = 293.8 ± 359.1), and the number of species from 7 to 128 (46.3 ± 26.8). The number of individuals recorded per species ranged widely from 1 to 1,385 (51.1 ± 124.2).

Despite our large sampling effort, individual-based rarefaction curves indicate that further surveys would be necessary to reach sampling sufficiency (i.e., to approach the asymptote of the curves; see Fig. S3). Completeness of the inventories per island ranged from 64 to 89% (73.6 ± 5.1; see Fig. S3). Since near-exhaustive inventories (> 80% completeness) were only obtained at four islands (see Fig. S3), the number of species in most surveyed islands should be regarded as conservative.

Species-area relationships and forest fragmentation effect

Island area had a significant positive effect on the number of species for all species, forest specialists, and habitat generalists (Fig. 2). The *z*-value for habitat generalists was significantly lower than for forest specialists ($P = 0.028$; Fig. 2), indicating that the rate of species loss as a function of island area reduction was higher for forest specialists.

The SAR models were deemed as appropriate to assess the forest fragmentation effect on avian species richness since the *z*-value was significant and the r^2_{adj} was ≥ 0.5 for all three datasets (Fig. 2). We recorded a higher overall number of species in surveyed islands than that extrapolated to an unfragmented forest area of 6,503 ha, the aggregate size of all 36 surveyed islands, considering both all species ($207 + 1 > 201.6$; Fig. 2a) and only habitat generalists ($124 + 1 > 104.7$; Fig. 2b). In contrast, this trend was reversed for forest specialists ($83 + 1 < 109.1$; Fig. 2c). However, the difference between the recorded and extrapolated number of species was not significant for all three datasets.

The Z-scores for all species (– 0.34), forest specialists (0.24), and habitat generalists (– 0.64) were not statistically significant, indicating that the structure of all three datasets could not be described as either anti-nested or nested (Fig. 2).

Trait-based vulnerability to forest fragmentation

Considering the observed PIO as a response variable, only the interactive PGLS 'rarity model' including natural abundance, habitat breadth, and geographic range size was highly supported based on AIC values (Table 2). This model explained most of the variance in observed PIO ($R^2_{adj} = 0.649$), outperforming the univariate PGLS models of natural abundance ($r^2_{adj} = 0.554$), habitat breadth ($r^2_{adj} = 0.031$), and geographic range size ($r^2_{adj} = 0.017$). Accordingly, species with higher abundance in pseudo-control islands (Fig. 3), broader habitat breadth, and wider geographic range tended to have higher values of observed PIO (see Fig. S4).

Considering the detectability-corrected PIO as a response variable, only the interactive PGLS 'rarity model' was highly supported based on AIC values (Table 2). This model explained a fifth of the variance in detectability-corrected PIO ($R^2_{adj} = 0.199$), outperforming the univariate models of natural abundance ($r^2_{adj} = 0.113$), habitat breadth ($r^2_{adj} = 0.047$), and geographic range size ($r^2_{adj} = 0.018$). Accordingly, species with higher

abundance in pseudo-control islands, broader habitat breadth, and wider geographic range tended to have higher values of detectability-corrected PIO (see Fig. S4).

Observed vs. detectability-corrected estimates of island occupancy

Vulnerability to forest fragmentation was widely variable across the 207 species in terms of the proportion of islands occupied (PIO), regardless of whether we considered observed or detectability-corrected PIO (see Table S3). The variation in observed PIO ranged from 2.8% to 94.4% (22.4 ± 22.5%), whereas the variation in detectability-corrected PIO ranged from 5.6% to 96.4% (42.4 ± 24.4%). Estimates of island occupancy corrected for imperfect detectability were higher than those observed for 200 species, identical for five, and slightly lower for two (see Table S3). For 30 species with detection probabilities below 30%, the detectability-corrected PIO was at least ten-fold higher than the observed PIO (16.0 ± 5.1%; Fig. 4; see Table S3). Conversely, differences between these two estimates were negligible or non-existent (1.02 ± 0.02%) for all 31 species with detection probabilities exceeding 45.5% (Fig. 4; see Table S3). Once phylogenetic non-independence was accounted for, detection probabilities was higher for more naturally abundant species ($r^2_{adj} = 0.206$, $P < 0.001$; Fig. 4).

DISCUSSION

Here we present one of the most comprehensive landscape-scale efforts to date to assess the role of morpho-ecological traits in explaining species vulnerability to forest fragmentation, in terms of the number of surveyed islands ($n = 36$), range of island sizes (3.4–2,551.5 ha), overall sampling effort ($n = 1{,}388$ samples), and number of species surveyed ($n = 207$). This effort exploited a quasi-experimental anthropogenic tropical forest archipelago, following an even-aged post-isolation history of 22-23 years, and allowed us to uncover which traits pose the greatest threats to bird species in forest islands embedded in hydroelectric reservoirs. We also highlight potentially misleading applications of species occupancy models by contrasting observed and detectability-corrected estimates of island occupancy.

Species-area relationships and forest fragmentation effect

Although SARs are arguably the most ironclad relationship in ecology (Rosenzweig, 1995), rates of species loss induced by declining habitat areas are highly variable. Triantis et al. (2012) synthesised 449 datasets from log-log SAR applications to islands in inland, continental-shelf and oceanic systems, and reported *z*-values ranging from 0.064 to 1.312 (mean ± SD = 0.321 ± 0.164). Such variance was attributed to several factors, namely island type, taxonomic group, and range of island areas (Triantis et al., 2012). A reliable comparison of *z*-values among studies should therefore take these factors into account.

Z-values derived for forest islands have been shown to be higher than for forest fragments (Matthews et al., 2016a), rendering forest fragmentation induced by hydroelectric dams (i.e. forest insularization) a more severe threat to biodiversity than that induced by agro-pastoral activities. We largely attribute such difference in *z*-values to the permeability of the intervening matrix, which may either preclude (increasing *z*-values; Moore et al., 2008) or allow species to disperse among forest patches, offsetting species losses through the rescue effect (decreasing *z*-values; Stouffer et al., 2009). For instance, in a fragmented southern Amazonian landscape dominated by cattle pasture – where 338 bird species were surveyed across 30 forest fragments (1–14,476 ha) – Lees & Peres (2008) derived a *z*-value of 0.191, which is considerably lower than in this study (0.316). Although we do not have direct evidence on species dispersal in these two landscapes, both studies are comparable in most factors affecting *z*-values (Triantis et al., 2012), except for the intervening matrix. Therefore, we predict that forest islands in existing and future hydroelectric reservoirs will experience a pronounced species richness decay, resulting in depauperate avian assemblages shaped by selective extinction (Mendenhall et al., 2014; Wolfe et al., 2015; Si et al., 2016).

Predictions of species losses based on the species-area relationship are affected by the degree of habitat specialisation of the species included in the analysis. In 16 out of 23 datasets, avian species richness decreased at a greater rate as a function of patch area reduction for forest specialists than habitat generalists (Matthews et al., 2014). Moreover, the inclusion of habitat generalist and edge species can even reverse the generally positive species-area relationship, whereby small patches will counter-intuitively harbour the most species-rich assemblages (Lovei et al., 2006). In archipelagic landscapes, colonisation of habitat generalists into forest islands is expected to be hindered by the aquatic matrix, ultimately reducing their impact on *z*-value estimates. In fact, our *z*-value derived for all species (0.316) approaches the mean value of island systems (0.321; Triantis et al., 2012) rather than that of terrestrial landscapes (0.202; Watling & Donnelly, 2006). However, our *z*-

464 value estimate for forest specialists (0.414) was significantly greater than that for habitat
465 generalists (0.262). Including habitat generalists in the species pool therefore reduced our
466 assemblage-wide rate of species loss, obscuring the more severe impact of habitat loss on
467 forest specialists, which reinforces the notion that habitat patches must be defined from the
468 perspective of target species (Lovei et al., 2006).

469 Forest fragmentation *per se* neither significantly decreased nor increased the overall
470 number of species predicted by forest loss (i.e. island area reduction) regardless of the dataset
471 used, which corroborates our prediction regarding the fragmentation effect on all species
472 (neutral) but not on both forest specialists (positive) and habitat generalists (negative).
473 Likewise, species richness was unrelated to fragmentation in previous studies undertaken in
474 different landscapes across a wide range of taxonomic groups. For instance, fragmentation
475 effects on the overall number of species in forest fragments were not evident for perennial
476 flowering plants and two beetle families in an agricultural landscape (Tenebrionidae and
477 Carabidae; Yaacobi et al., 2007), and for butterflies in an urban landscape (Soga & Koike,
478 2012). Yet this failed to hold true for lizards in an archipelagic landscape, where the overall
479 number of species in forest islands was significantly decreased by fragmentation (Wang et
480 al., 2009). Hypothetically, terrestrial matrices can then buffer fragmentation effects as they
481 are more permeable to species movements than water matrices (Soga & Koike, 2012), or
482 even increase gamma diversity as shown for spider species in forest fragments of two
483 agricultural landscapes in Israel (Gavish et al., 2012). To test this hypothesis, we reanalysed
484 the bird data available from the Thousand Island Lake forest archipelago in China (Si et al.,
485 2015) applying the same analysis carried out here (Yaacobi et al., 2007). We found no
486 support for that hypothesis since forest fragmentation *per se* significantly increased the
487 overall number of bird species in forest islands (60 recorded > 42.6 extrapolated; see Fig.
488 S5), which is partially explained by the low *z*-value (0.098; see Yu et al., 2012) and the anti-
489 nested structure (Si et al., 2015) of the avian assemblages in the Thousand Island Lake
490 (Santos et al., 2010; Matthews et al., 2016b). Accordingly, anti-nested assemblages (i.e.
491 species present at an island are not present at other islands) are expected to have a higher
492 gamma diversity than nested assemblages (i.e. species present in smaller islands are subsets
493 of larger islands; Santos et al., 2010), ultimately determining the direction (positive or
494 negative) and magnitude of the fragmentation effect on species richness. In this study, the
495 lack of fragmentation effects on species richness of the datasets including all species, forest
496 specialists, and habitat generalists was thus unsurprisingly given the non-significant nested

structure of these avian assemblages. Collectively, this indicates that the extrapolation of SAR models is an indirect method to infer the nested structure of species assemblages (this study; Santos et al., 2010; Matthews et al., 2016b).

In a recent SLOSS-type analysis, Fahrig (2017) uncovered a significantly higher overall number of species in several small patches compared to a single large patch based on 60 compiled datasets. This suggests that habitat fragmentation *per se* increases the overall number of species in habitat patches, but we caution against such assertion for three reasons. First, anti-nested assemblages are shaped by species turnover, which depends on landscape-dispersal processes determined by isolation (with lower isolation leading to greater anti-nested structure; Santos et al., 2010), matrix permeability (Stouffer et al., 2011), and species dispersal capacity (Si et al., 2014). Second, methodological choices may lead to biased outcomes as exemplified by the nested structure of species assemblages in fragmented landscapes (Watling & Donnelly, 2006), though a meta-analysis including 97 datasets deemed these an analytical artefact since most species assemblages are neither significantly anti-nested nor nested (Matthews et al., 2015). Since fragmentation effects on species richness are strictly related to the nested structure of species assemblages, we believe that a fragmentation effect on species richness would not be evident for most studies compiled by Matthews et al. (2015). This contradicts Fahrig's (2017) conclusions, which were largely grounded on the positive fragmentation effect on species richness when comparing between species accumulation curves of sites ordered according to either increasing or decreasing patch area (Quinn & Harrison, 1988). Nevertheless, this method is biased towards detecting higher species richness in several small patches compared to a single large patch due to unequal sampling intensity (i.e. proportion of patch area that is surveyed) among surveyed patches (Gavish et al., 2012). Third, an assemblage-level approach may mask fragmentation effects on individual species, since measures of species richness completely disregard species identity.

Trait-based vulnerability to forest fragmentation

Rarity is an intrinsic property of certain species that results from variable cross-scale combinations of small local population size, restricted habitat breadth, and narrow geographic range (Rabinowitz, 1981). Rare species are inherently predisposed to high extinction risk, which justifies the use of rarity as a measure of species vulnerability to a wide range of

anthropogenic stressors (Kattan, 1992; Mace et al., 2008). Using a global-scale analysis, Newbold et al. (2014) reported that forest specialists and narrow-range bird species from tropical and sub-tropical forest biomes are more vulnerable to land-use change than habitat generalists and wide-range species. We corroborate this outcome at the scale of an archipelagic landscape, and endorse other comparative analyses incorporating field data (i.e. estimates of local population size; Feeley et al., 2007) and synergistic interactions among ecological traits that amplify the power of predictive models (Wang et al., 2015). Moreover, we identified rarity as a decisive factor exacerbating species vulnerability at all three spatial dimensions defined by Rabinowitz (1981), particularly because rarity is unrelated to several key traits, such as body mass and flocking behaviour (Thiollay, 1994; but see Kattan, 1992). As such, species with higher natural abundance, broader habitat breadth and wider geographic range were those with the highest rates of island occupancy at the THR landscape. Nevertheless, natural abundance played a disproportionately important role compared to habitat breadth and geographic range size, a pattern corroborated in another Amazonian fragmented landscape (Lees & Peres, 2008). A positive abundance-occupancy relationship, in which more abundant species occupy more sites, is widely considered a general rule in ecology (Hartley, 1998). Although many underlying mechanisms have been proposed to explain this relationship, there is no broadly accepted consensus as to why locally abundant species should be more ubiquitous (Gaston et al., 2000). We stress that our findings can be extended to other fragmented landscapes, including those dominated by variable-quality terrestrial matrices, in which non-random extirpations could also be predicted by metrics of rarity.

Based on our PGLS models, we failed to find support for some ecological traits that are often associated with avian extinction risk in human-modified tropical forest landscapes, namely body mass, trophic level, vertical foraging stratum, and flocking behaviour (Sodhi et al., 2004). However, this does not imply that these traits are not meaningful (Hamer et al., 2015), although body mass, foraging specialisation, and vertical stratum were unrelated to bird species vulnerability in a fragmented Atlantic Forest of southern Brazil (Anjos, 2006). In some instances, the role of species traits in predicting vulnerability to forest fragmentation depends on the scale (global vs. landscape) and the response variable (e.g. population size vs. global extinction risk scores) used in the study (Keinath et al., 2017). For example, body mass has been often reported as a meaningful trait in broad-scale studies using global extinction risk scores (Keinath et al., 2017). Moreover, in model selection approaches, the

562 best-fit models depend on the entire set of plausible competitive models (Aho et al., 2014).
563 Had we considered only univariate models including each of those four traits separately, body
564 mass ($\Delta AIC \leq 2$ in this instance) would have emerged as the most important ecological trait
565 in explaining observed island occupancy rates (Table 2), with small-bodied species
566 occupying more islands than large-bodied species ($r^2_{adj} = 0.015$). Any given trait or
567 combination of traits may therefore play a role in a comparative analysis, but collectively
568 may operate as less meaningful variables (Keinath et al., 2017). Furthermore, the large
569 number of species included in the analysis ($n = 207$) can obscure the role of ecological traits
570 associated with only a few species (e.g. obligate ant-followers, $n = 2$), since the deviance of a
571 few values may change the balance of strength in competing traits but not the main outcome.

572 It has been widely reported that insectivore species are particularly vulnerable to
573 forest fragmentation (Bregman et al., 2014; Powell et al., 2015), especially ground
574 insectivores (Stratford & Stouffer, 1999) and obligate flocking species (i.e. mixed-species
575 flock attendants and ant-followers; Van Houtan et al., 2006). Hence, species at higher trophic
576 levels, using lower forest strata, and joining flocks were expected to exhibit lower rates of
577 island occupancy. We failed to corroborate these expectations, which we largely attribute to
578 differences in sampling design and analytical approaches among studies (Powell et al., 2015).
579 For example, in an anthropogenic tropical forest archipelago in Malaysia, avian insectivores
580 showed the steepest decline in the number of species with decreasing island area compared to
581 either omnivores or frugivores (Yong et al., 2011). Had we applied the semi-log form of the
582 species-area relationship [$S \sim \log_{10}(A)$] to the same three avian foraging guilds, as the authors
583 did, we would also have identified insectivores (*sensu* Wilman et al., 2014) as the most
584 impaired foraging guild (see Fig. S6). To provide further evidence of the impact of the
585 analytical approach on the outcomes, we additionally applied the log-log form of the species-
586 area relationship to both our dataset and the dataset available from the Malaysian archipelago
587 (Yong et al., 2011). Although the outcomes converged between studies, frugivores emerged
588 as the most impaired foraging guild, rather than insectivores (see Fig. S6). Another
589 noteworthy point is that species grouped into a foraging guild may span more than an entire
590 trophic level (Hamer et al., 2015). As such, the trophic level of an insectivore species could
591 overlap that of a carnivore (Hamer et al., 2015), omnivore, or granivore species (see Fig. S7).
592 In Bornean rainforests, insectivore species showed variable responses to selective logging,
593 with species at higher trophic levels more adversely affected than those at lower trophic
594 levels (Hamer et al., 2015). These authors used stable isotopes to quantify trophic levels, a

more accurate approach than our energetic score, preventing a direct comparison between studies.

Ground insectivores were extirpated from small Amazonian forest remnants (≤ 10 ha) following fragmentation (Stratford & Stouffer, 1999) since edge-dominated remnants could no longer sustain critical foraging microhabitats for these species (Stratford & Stouffer, 2013). Likewise, none of the five ground insectivores we recorded (*Conopophaga aurita*, *Conopophaga roberti*, *Formicarius analis*, *Formicarius colma*, and *Hylopezus macularius*) was found in islands smaller than 30 ha (see Fig. S8). Moreover, obligate flocking species were extirpated from small fragments (1–10 ha) after isolation (Stouffer & Bierregaard, 1995), a pattern corroborated at the THR landscape, where smaller islands also harboured depauperate assemblage of these social species (see Fig. S8). Although mixed-species flocks and obligate ant-followers can reassemble and recolonize small fragments following the regrowth of the intervening matrix (Stouffer & Bierregaard, 1995; Stouffer et al., 2011), these rebounds, by definition, cannot occur within hydroelectric reservoirs. Finally, the only comparable avian island biogeography study (Thousand Island Lake, China; Wang et al., 2015) – in terms of both the sampling design and analytical approach used here – is largely consistent with our findings, in which only natural abundance and habitat breadth had sufficiently high support in explaining species occupancy patterns in forest islands.

Observed vs. detectability-corrected estimates of island occupancy

Occupancy modelling is assumed to derive more reliable estimates of patch occupancy as it accounts for potentially present species that go undetected in a given patch (MacKenzie et al., 2002). As a result, estimates of patch occupancy corrected for imperfect detectability are, as a general rule, equal to or higher than observed estimates (this study; Thornton et al., 2011; Wang et al., 2015). In an archipelagic landscape created by China's Thousand Island Lake, detectability-corrected proportions of islands occupied were up to seven-fold higher than that observed for a small raptor (*Accipiter soloensis*; Wang et al., 2015). At the THR landscape, those estimates were at least ten-fold higher for 31 bird species, and almost 29-fold higher for two additional species (Fig. 5; see Table S3). These large discrepancies can be explained by overestimates of patch occupancy for species with detection probabilities lower than 30% (MacKenzie et al., 2002). Overcoming this artefact to obtain more reliable estimates of patch

626 occupancy would require increasing the number of samples per patch, but this is not always
627 feasible due to logistical constraints (Mackenzie & Royle, 2005).

628 Estimates of patch occupancy for species with low detection probabilities (< 30%)
629 can be misleading and the large uncertainties they carry should be interpreted with caution
630 (Welsh et al., 2013). Such species may be defined as ubiquitous due to overestimates of patch
631 occupancy, even though they have been recorded at only a few patches (Banks-Leite et al.,
632 2014), which would invalidate species-specific predictions of vulnerability based on rates of
633 patch occupancy. This was the case for *Myiopagis caniceps* and *Psarocolius bifasciatus*,
634 which were recorded in only one island but were estimated to occupy 29. As species
635 detectability tends to increase with increasing natural abundance, occupancy models yield far
636 more reliable estimates of patch occupancy for common species than those that are rare
637 (Banks-Leite et al., 2014). Because over 200 species distributed across many lineages were
638 considered in this study, identifying morpho-ecological characteristics that can best explain
639 species vulnerability to forest fragmentation was largely unbiased. However, the same cannot
640 be stated for species-poor assemblages in which most species have low detection
641 probabilities. We argue that estimates of detectability-corrected proportions of patches
642 occupied should always be reported and examined together with species detectability and
643 observed estimates, to avoid misleading assessments of species vulnerability based on rates
644 of patch occupancy.

645

646 **CONCLUSIONS**

647 On the basis of a comprehensive bird survey undertaken in forest islands within a major
648 Amazonian hydroelectric reservoir, we addressed four questions: (1) Do habitat generalists
649 show a less steep decline in species richness as a function of island area reduction compared
650 to forest specialists? (2) Does forest fragmentation *per se* exacerbate or reduce the impact of
651 forest loss on species richness for the overall species pool, forest specialists, and habitat
652 generalists? (3) Which suite of morpho-ecological traits best explains species rates of island
653 occupancy within the forest archipelago? (4) How divergent are observed and detectability-
654 corrected estimates of island occupancy for rarely detected species? Our findings show that
655 (1) rates of species loss of forest specialists in land-bridge islands are underestimated if
656 habitat generalists are included in the species pool because habitat generalists are less
657 impacted by island area reduction than forest specialists; (2) fragmentation *per se* does not

necessarily exacerbate the effects of forest loss on species richness; (3) rare species, especially those with low natural local abundance, are the most extinction-prone in fragmented landscapes; and (4) detectability-corrected estimates of island occupancy can be much higher than observed estimates for species with low detection probability, ultimately limiting the use of occupancy models for rare or elusive species. Finally, we conclude that forest islands within hydroelectric reservoirs are expected to typically harbour depauperate avian assemblages, mostly consisting of naturally abundant and habitat generalist species.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Details on estimates of local extinctions.

Figure S1 Distribution of point count stations (PCs) in pseudo-control islands.

Figure S2 Comparison between the number of species in pseudo-control islands and in treatment islands.

Figure S3 Individual-based rarefaction curves.

Figure S4 Relationships between the proportion of islands occupied and species traits.

Figure S5 Species-area relationships for birds at the Thousand Island Lake in China.

Figure S6 Comparison of species-area relationships for three avian foraging guilds within two archipelagic landscapes.

Figure S7 Distribution of trophic level scores according to avian foraging guild.

Figure S8 Species occurrence of ground insectivores, obligate ant-followers, and obligate mixed-species flock attendants along the island area gradient.

Table S1 Description and number of bird species within the 36 surveyed islands at the THR landscape.

Table S2 Description and sources of seven avian morpho-ecological traits for all species considered in this study.

Table S3 Morpho-ecological traits of bird species and estimated proportion of islands occupied.

BIOSKETCH

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FIGURE LEGENDS

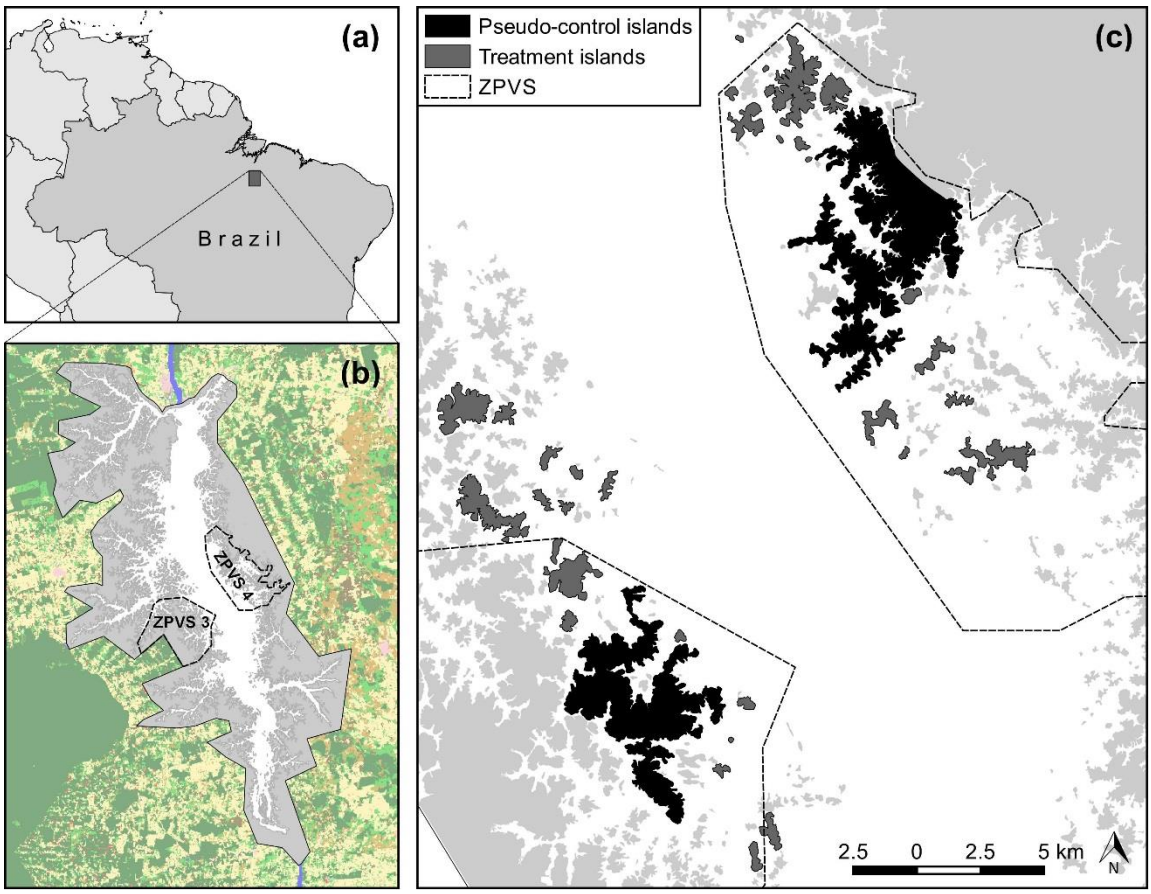
Figure 1 (a) Location of the study area in eastern Brazilian Amazonia; (b) Tucuruí Hydroelectric Reservoir (THR) within the Tucuruí Lake Environmental Protection Area (grey and white areas), showing the two Wildlife Conservation Zones (ZPVS 3 and 4, indicated by dotted lines) and heavily degraded areas surrounding the reservoir (yellow); and (c) distribution of the 36 surveyed islands (dark grey and black polygons) within or adjacent to the two ZPVS. The background image was extracted from the TerraClass project (Almeida et al., 2016), available at <http://www.inpe.br/cra/projetos_pesquisas/terraclass2008.php>. [Colour figure can be viewed at wileyonlinelibrary.com]

Figure 2 Plots at the top show the species-area relationships, and their r^2- and *z*-values for (a) all species; (b) forest specialists; and (c) habitat generalists surveyed across 36 islands at the THR landscape ($P < 0.001$ in all instances). Dotted lines indicate null predicted numbers of species if forest fragmentation had no effect. Circles, squares, and triangles correspond to the recorded, extrapolated, and overall number of species, respectively. Coloured regions and error bars show the 95% confidence intervals of predicted lines and extrapolated values, respectively. Note the base 10 logarithmic scales along both axes. Plots at the bottom show the maximally packed matrices for (d) all species; (e) forest specialists; and (f) habitat generalists based on the NODF nestedness metric (Almeida-Neto et al., 2008). Coloured bars indicate the islands (*x*-axis) where each species (*y*-axis) was recorded. None of the datasets was either significantly nested or anti-nested. [Colour figure can be viewed at wileyonlinelibrary.com]

Figure 3 Site-by-species abundance matrix for 207 bird species surveyed across 36 islands at the THR landscape. Squares representing at least a single individual detected per site are colour-coded according to the respective natural abundance of each species, defined as the total number of individuals recorded within pseudo-control islands. Islands are ordered from the largest to the smallest; species are ordered from the most to the least ubiquitous in terms of observed proportion of islands occupied. [Colour figure can be viewed at wileyonlinelibrary.com]

Figure 4 Ratio between detectability-corrected and observed estimates of proportion of islands occupied as a function of species detectability for 207 bird species surveyed across 36 islands at the THR landscape; *y*-values indicate how many times detectability-corrected estimates are higher than observed estimates. Species symbols are colour-coded according to the total number of individuals recorded within pseudo-control islands. [Colour figure can be viewed at wileyonlinelibrary.com]

1017 **FIGURES**



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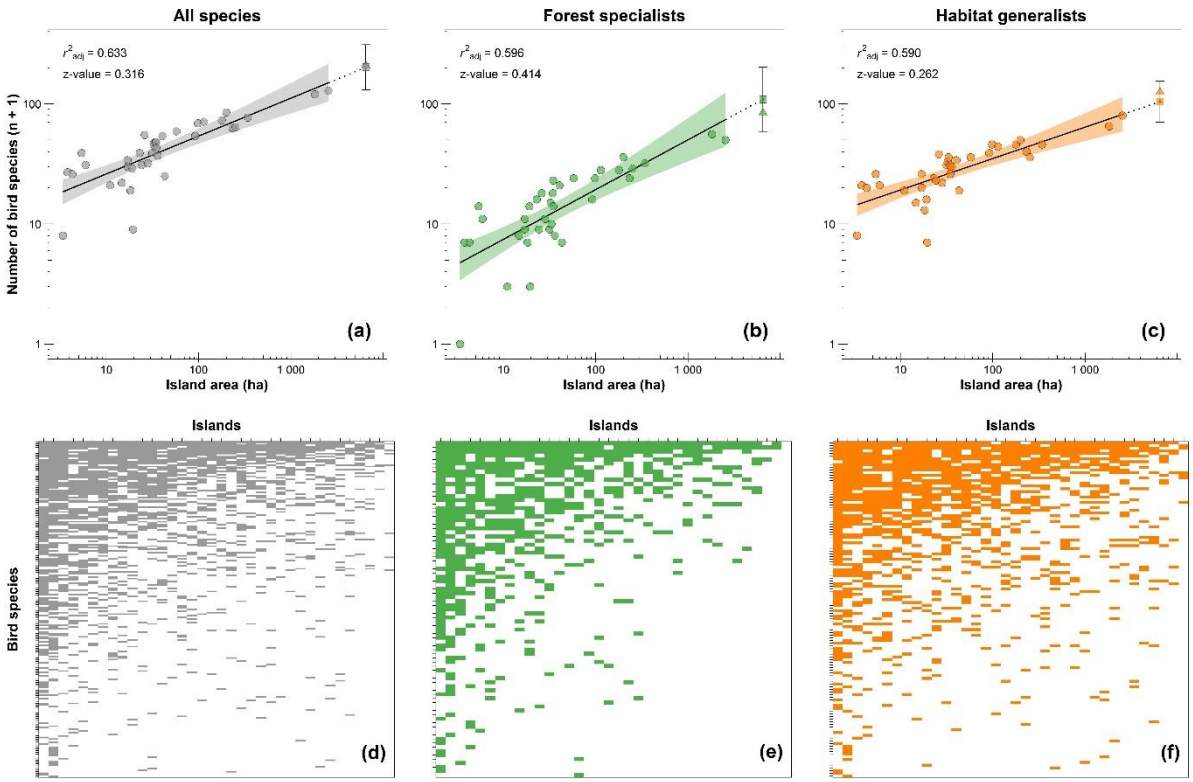

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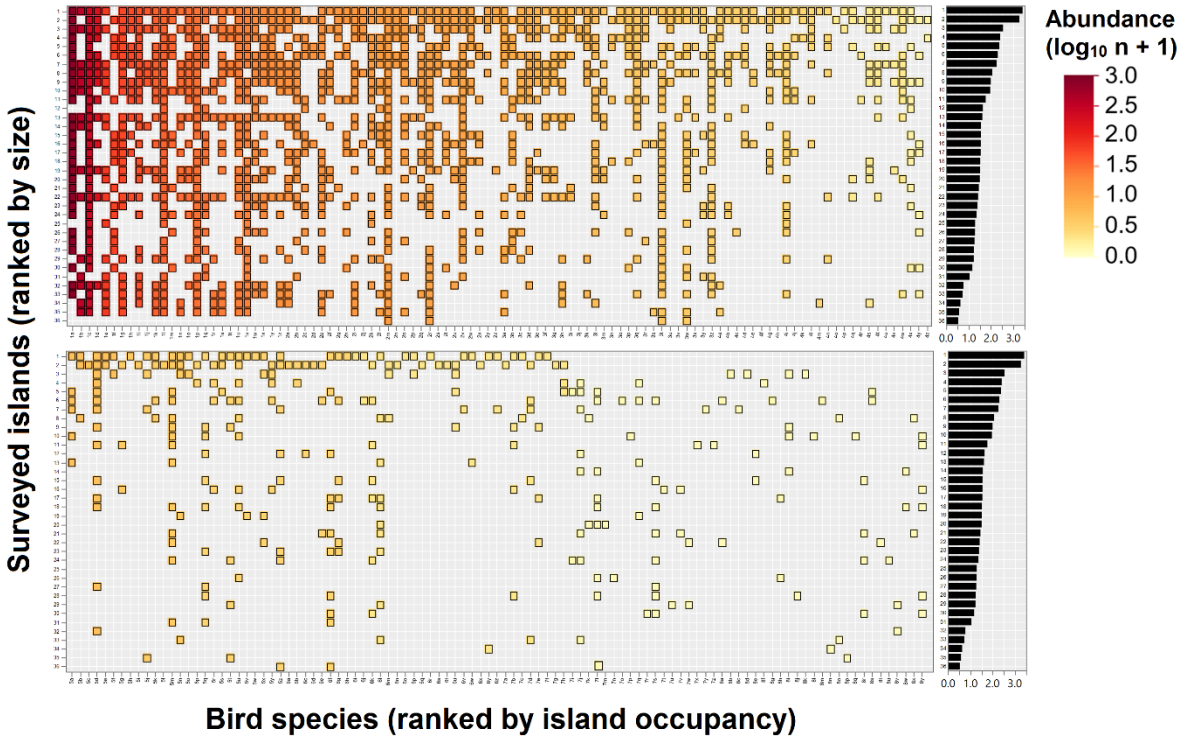

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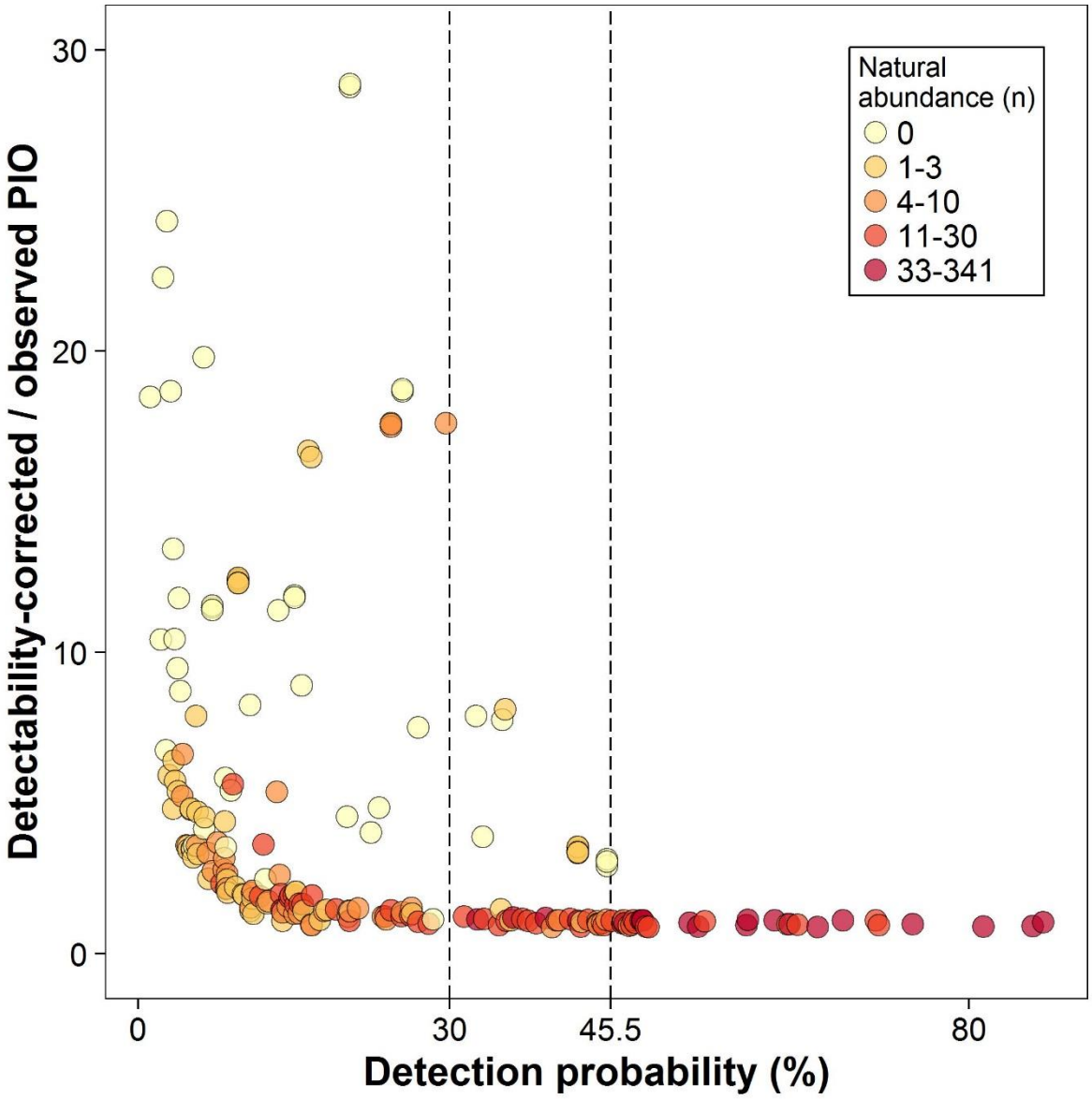

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1028 Figure 4

TABLES

Table 1 Structure of the 16 occupancy models used to estimate detectability-corrected proportions of islands occupied for 207 bird species surveyed across 36 islands at the THR landscape. Probability of occupancy (ψ) was modelled as a function of $\log_{10}$ island area in hectares (AREA), shape index (SHAPE), and proximity index (PROX). The probability of detection (p) was modelled as a function of the number of point count stations surveyed per island (EFFORT).

Model description
$\psi(.)\ p(.)$
$\psi(\text{AREA})\ p(.)$
$\psi(\text{SHAPE})\ p(.)$
$\psi(\text{PROX})\ p(.)$
$\psi(\text{AREA} \times \text{SHAPE})\ p(.)$
$\psi(\text{AREA} + \text{PROX})\ p(.)$
$\psi(\text{SHAPE} + \text{PROX})\ p(.)$
$\psi(\text{AREA} \times \text{SHAPE} + \text{PROX})\ p(.)$
$\psi(.)\ p(\text{EFFORT})$
$\psi(\text{AREA})\ p(\text{EFFORT})$
$\psi(\text{SHAPE})\ p(\text{EFFORT})$
$\psi(\text{PROX})\ p(\text{EFFORT})$
$\psi(\text{AREA} \times \text{SHAPE})\ p(\text{EFFORT})$
$\psi(\text{AREA} + \text{PROX})\ p(\text{EFFORT})$
$\psi(\text{SHAPE} + \text{PROX})\ p(\text{EFFORT})$
$\psi(\text{AREA} \times \text{SHAPE} + \text{PROX})\ p(\text{EFFORT})$

Table 2 Performance of 13 Phylogenetic Generalised Least Squares (PGLS) models relating either observed or detectability-corrected estimates of island occupancy to seven morpho-ecological traits, and combinations thereof, for 207 bird species surveyed across 36 islands at the THR landscape.

Model description	**degrees of freedom**	**AIC**	**ΔAIC**	**ω_i**	**R^2_{adj}**
Response variable: observed proportion of islands occupied					
Univariate models					
Natural abundance	2	1697.156	43.914	2.906×10^{-10}	0.554
Habitat breadth	2	1847.339	194.097	7.106×10^{-43}	0.031
Geographic range size	2	1850.609	197.367	1.385×10^{-43}	0.017
Body mass	2	1851.324	198.082	9.692×10^{-44}	0.015
Flocking behaviour	2	1854.164	200.922	2.342×10^{-44}	-0.001
Vertical stratum	2	1854.457	201.215	2.023×10^{-44}	-0.002
Trophic level	2	1854.859	201.617	1.654×10^{-44}	-0.004
Additive models					
Rarity: natural abundance + habitat breadth + geographic range size	4	1666.012	12.770	0.0016838	0.620
Population size: natural abundance + body mass + trophic level	4	1700.695	47.453	4.953×10^{-11}	0.551
Foraging: trophic level + vertical stratum + flocking behaviour	4	1857.686	204.444	4.024×10^{-45}	-0.007
Interactive models					
Rarity: natural abundance × habitat breadth × geographic range size	8	1653.242	0	0.9983161	0.649
Population size: natural abundance × body mass × trophic level	8	1703.476	50.234	1.233×10^{-11}	0.553
Foraging: trophic level × vertical stratum × flocking behaviour	8	1862.862	209.620	3.026×10^{-46}	-0.015
Response variable: detectability-corrected proportion of islands occupied					
Univariate models					
Natural abundance	2	1877.108	15.115	4.064×10^{-04}	0.113
Habitat breadth	2	1891.956	29.963	2.425×10^{-07}	0.047
Geographic range size	2	1898.313	36.320	1.010×10^{-08}	0.018
Body mass	2	1901.068	39.075	2.548×10^{-09}	0.159
Trophic level	2	1902.068	40.075	1.545×10^{-09}	-0.001
Flocking behaviour	2	1902.322	40.329	1.361×10^{-09}	-0.002
Vertical stratum	2	1902.809	40.816	1.066×10^{-09}	-0.004
Additive models					
Rarity: natural abundance + habitat breadth + geographic range size	4	1864.517	2.524	0.2203897	0.173
Population size: natural abundance + body mass + trophic level	4	1875.749	13.756	0.0008020	0.128
Foraging: trophic level + vertical stratum + flocking behaviour	4	1905.499	43.506	2.779×10^{-10}	-0.008
Interactive models					
Rarity: natural abundance × habitat breadth × geographic range size	8	1861.993	0	0.7782599	0.199
Population size: natural abundance × body mass × trophic level	8	1879.219	17.226	0.0001414	0.130
Foraging: trophic level × vertical stratum × flocking behaviour	8	1909.821	47.828	3.202×10^{-11}	-0.010

SUPPORTING INFORMATION

Appendix S1 Details on estimates of local extinctions.

The use of estimates of island occupancy (i.e. proportion of islands occupied – PIO) as a measure of species vulnerability to forest fragmentation is only meaningful if local extinctions have occurred at the study islands (Bolger et al., 1991; Keinath et al., 2017). Ideally, bird surveys would be carried out at the time of island creation, which could be compared with present-day species distributions to determine the occurrence of local extinctions (Bolger et al., 1991). In the absence of historical data, which is typically the case in ecological studies, the comparison between species-area relationships (SARs) for birds in pseudo-control islands and in treatment islands can be alternatively used to infer the occurrence of local extinctions across study islands (Brown, 1971; Bolger et al., 1991; Wang et al., 2009). As such, bird surveys were carried out in pseudo-control islands within plots of similar size to those in treatment islands to represent species distributions in an unfragmented habitat (Bolger et al., 1991; Wang et al., 2009).

To produce the species-area curves for both pseudo-control islands and treatment islands, we used the number of bird species recorded as a function of surveyed area rather than total island area to make the spatial extent of radial surveys around point-count stations comparable in both pseudo-control islands and treatment islands (Wang et al., 2009). Only species that had been recorded in pseudo-control islands (n = 164) were considered for this comparison. For example, one of the seven species recorded at our smallest site (3.39 ha), Island Caua (Table S1), was not recorded in pseudo-control islands, so the number of species in that island was restricted to six. Surveyed areas (expressed in hectares) were calculated as the survey area of a point-count station ($\pi \times 50^2$; hereafter, PCs) times the number of PCs sampled. For instance, the surveyed area within Island Caua was 1.57 ha as we deployed two PCs in that island, each of which covering an area of 0.785 ha.

For treatment islands, each island was considered as a data point (n = 34) with the total number of species recorded defined as the dependent variable and total surveyed area as the independent variable (blue circles in Fig S2a). In contrast, for pseudo-control islands, we used the mean number of species recorded in each of the six survey transects placed therein (Fig. S1) as the dependent variable, which was calculated from the aggregated number of species recorded across all possible combinations of adjacent PCs (Fig. S1) for any given area surveyed (i.e. independent variable) in treatment islands. As such, the total survey area

was held constant in both pseudo-control and treatment islands. For example, to calculate the mean number of species along the transect Pedral-B (which contained only five PCs; Fig. S1) for an area equivalent to two adjacent PCs (1.57 ha), we used the number of species recorded by pairing PCs 1-2, 2-3, 3-4 and 4-5 (Fig. S1). In this case, the number of species recorded was 38, 40, 49 and 45, respectively, with a mean of 43 species. We followed the same procedure for all transects and combinations of 2, 3, 4, 6, 8, 10, 11 and 13 adjacent PCs, amounting to 33 data points (red circles in Fig. S2a). Subsequently, we performed an ANCOVA model with island type as the categorical independent variable to determine whether the intercept (*c*-value) and the slope (*z*-value) of the predicted lines (red and blue lines in Fig. S2a) were statistically different.

Predicted lines derived from pseudo-control islands ($r^2_{adj} = 0.950$, $P = 0.001$) and from treatment islands ($r^2_{adj} = 0.614$, $P = 0.001$) were different in both the *c*-values ($P < 0.001$) and *z*-values ($P = 0.008$). For treatment islands, the *c*-value was 1.125 and the *z*-value was 0.745. For pseudo-control islands, the *c*-value was 1.533 and the *z*-value was 0.450. As such, treatment islands only supported depauperate species assemblages and had experienced a much higher rate of species loss as a function of surveyed area in relation to equivalent-sized survey areas within pseudo-control islands, which indicates that local extinction had indeed occurred in treatment islands.

To estimate the number of extinctions that had occurred in treatment islands, we rounded down the predicted number of species in pseudo-control islands (red line in Fig. S2a) to the nearest integer which was subtracted from the number of species recorded in treatment islands (blue circles in Fig. S2a; Bolger et al., 1991). For example, the estimated number of local extinctions at the small Island Caua was 35, since the predicted number of species in pseudo-control islands for an equivalent survey area of 1.57 ha was 41.85, whereas the recorded number of species in that island was only 6 (Fig. S2b). Overall, we estimated that a total of 788 local extinctions had occurred across all 34 treatment islands over 22-23 years of post-isolation history at the Tucuruí Hydroelectric Reservoir landscape.

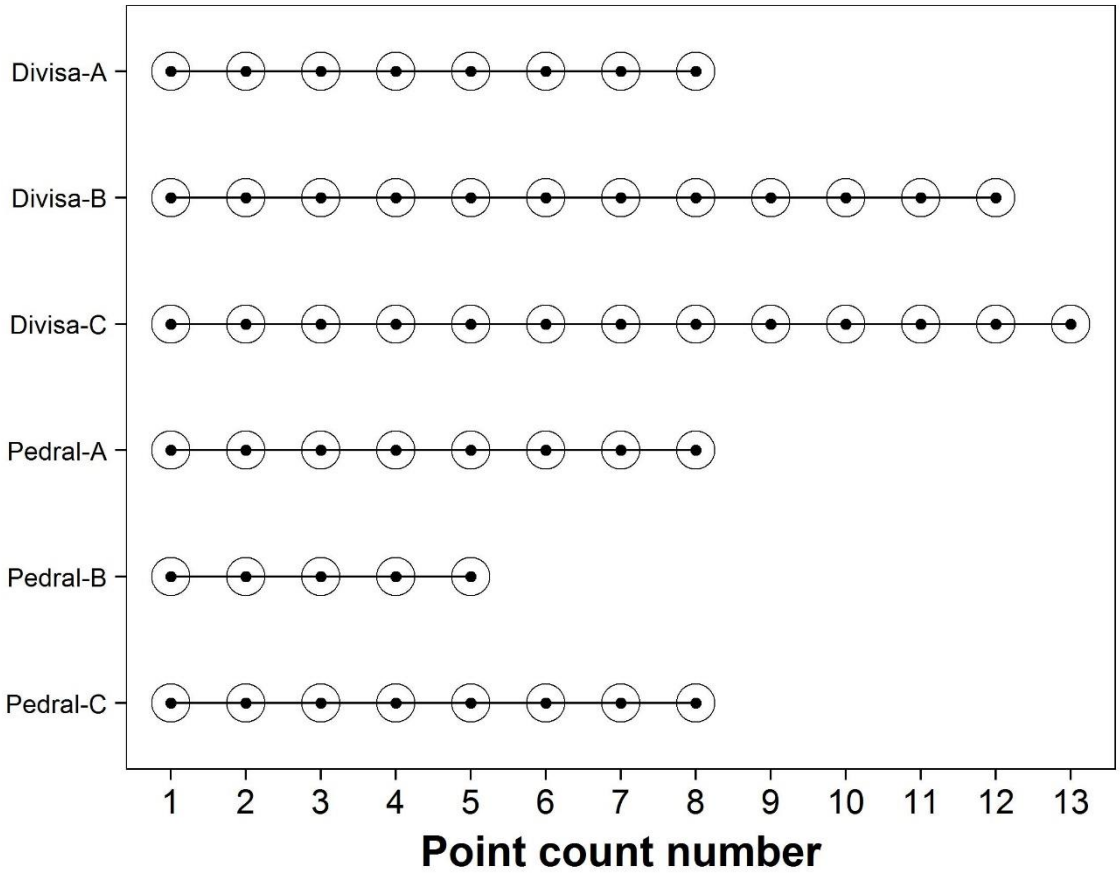


Figure S1 Schematic representation of all six transects and 54 point count stations (PCs) deployed within the two very large pseudo-control islands (Divisa and Pedral). PCs (black dots) and their 50-m fixed-radius survey areas (circles) were distributed at regular 200-m intervals along transects (black lines).

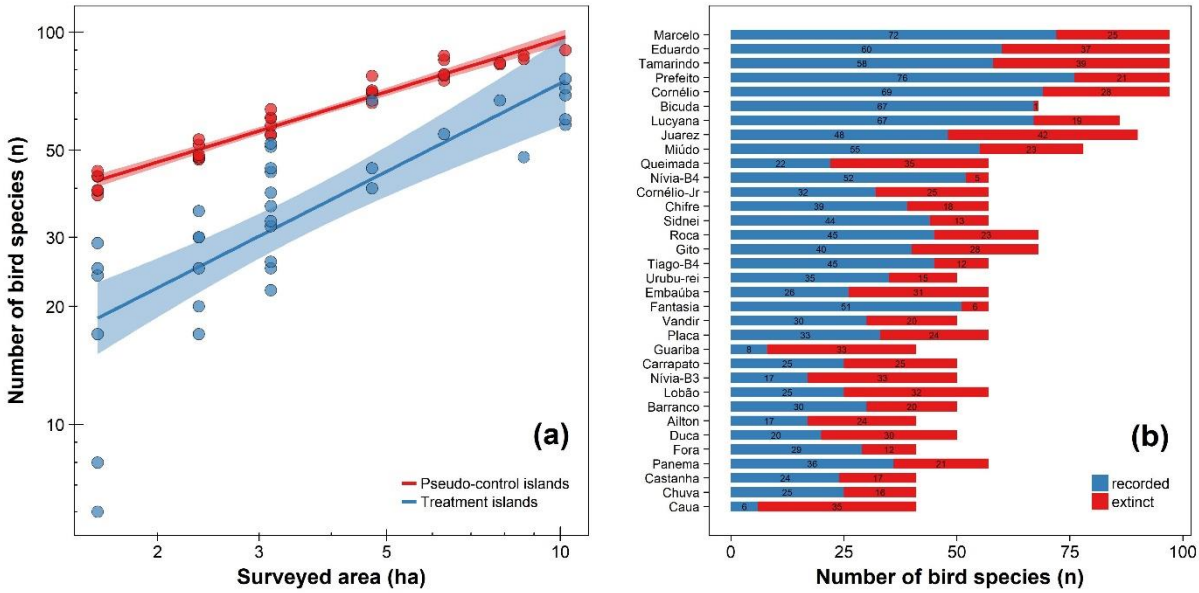


Figure S2 (a) Species-area relationships for birds in pseudo-control islands (red lines and circles) and in treatment islands (blue lines and circles) as a function of surveyed area around point count stations. Coloured regions show the 95% confidence intervals of predicted lines. (b) Numbers of bird species within pseudo-control islands (n = 164) that were either recorded (blue horizontal bars) or estimated to have been extirpated following isolation across 34 treatment islands at the THR landscape (red horizontal bars). Islands are ordered top to bottom from the largest to the smallest (Table S1). Note the base 10 logarithmic scales along both axes.

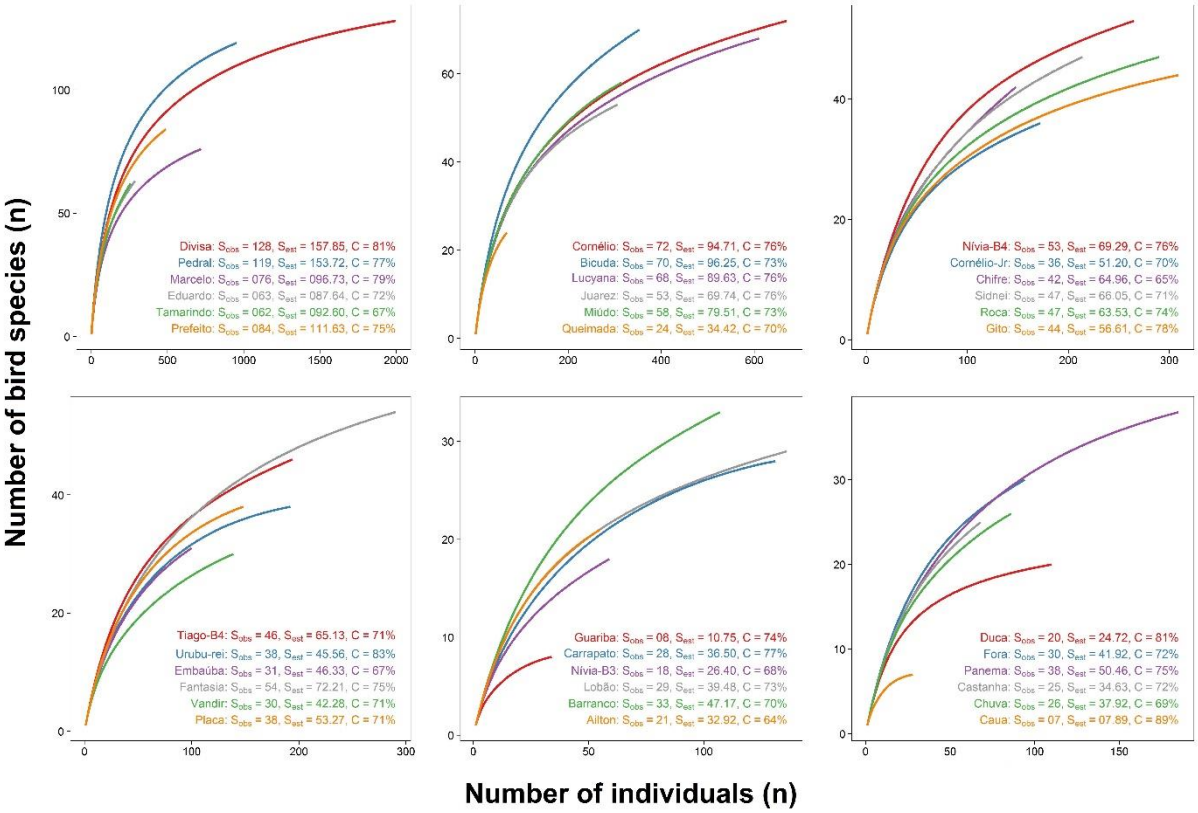
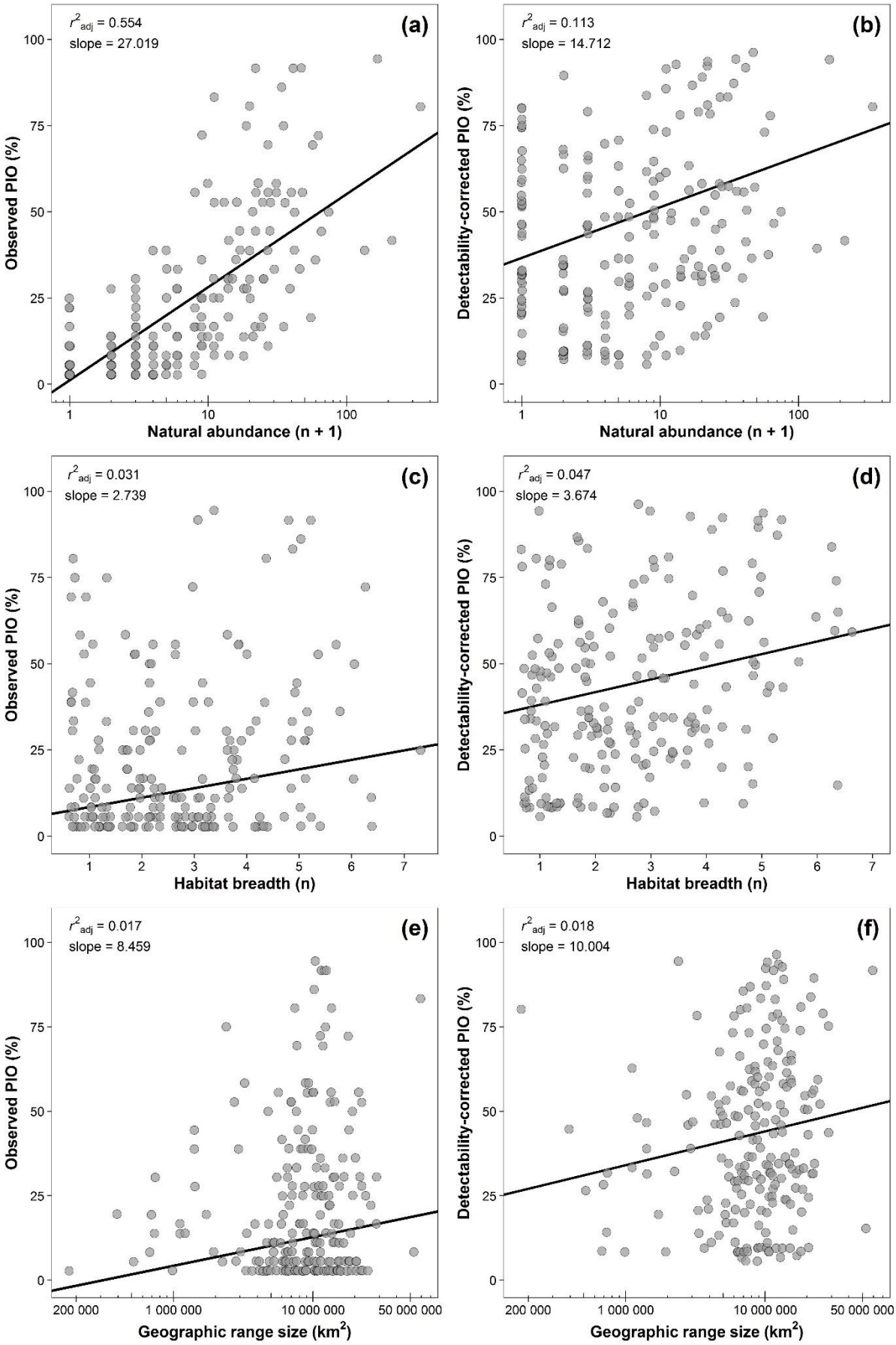
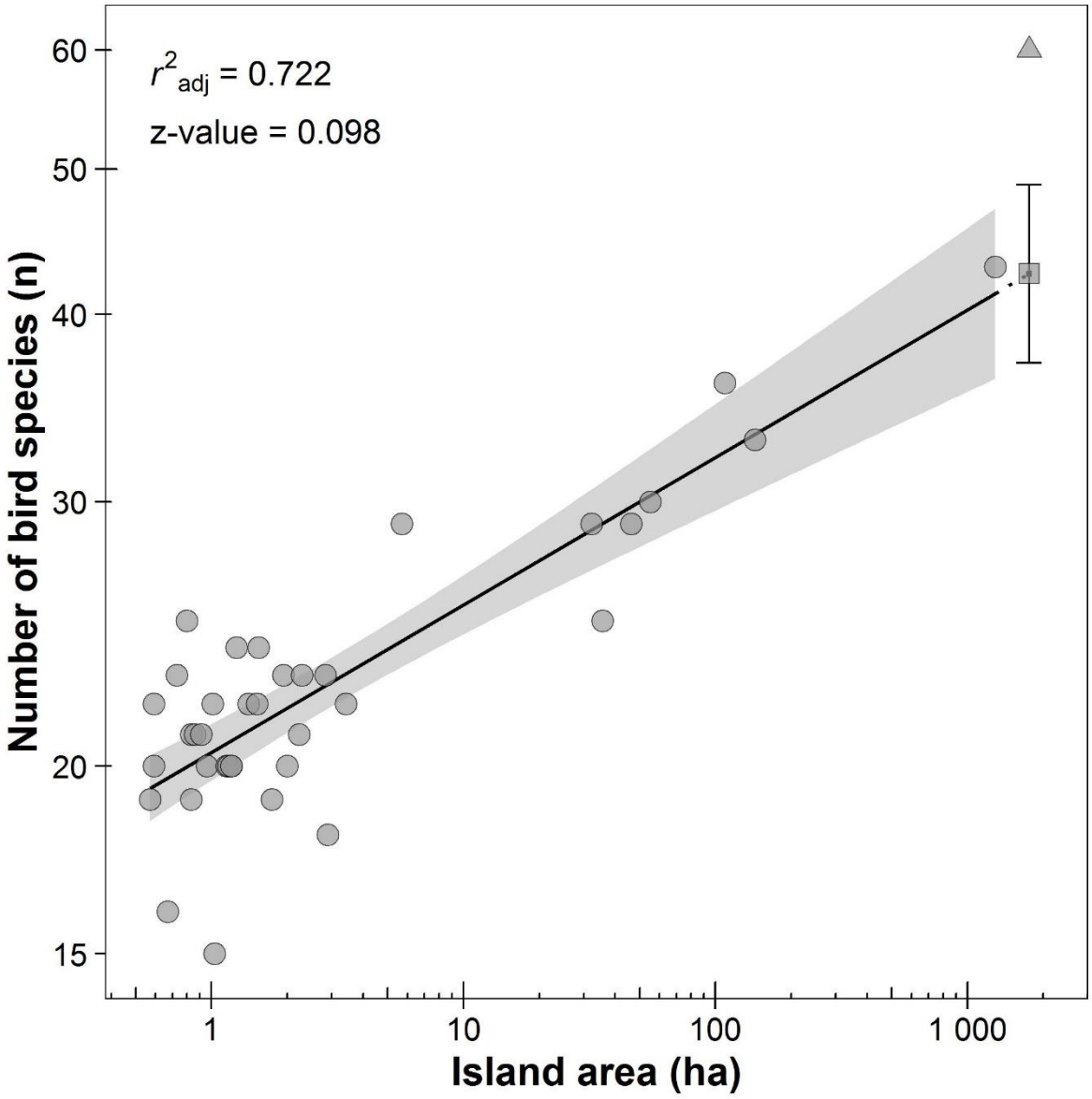


Figure S3 Individual-based rarefaction curves of the number of bird species recorded per surveyed island at the THR landscape. Each line represents one island coloured according to its sampling completeness, which was quantified as a percentage between the observed recorded and the estimated number of species based on the first-order Jackknife estimator. Islands are ordered by decreasing size as in Table S1. Note the different scales on both the *x* and *y* axes.


(a)
r^2_{adj} = 0.554
slope = 27.019
Observed PIO (%)
Natural abundance (n + 1)
(b)
r^2_{adj} = 0.113
slope = 14.712
Detectability-corrected PIO (%)
Natural abundance (n + 1)
(c)
r^2_{adj} = 0.031
slope = 2.739
Observed PIO (%)
Habitat breadth (n)
(d)
r^2_{adj} = 0.047
slope = 3.674
Detectability-corrected PIO (%)
Habitat breadth (n)
(e)
r^2_{adj} = 0.017
slope = 8.459
Observed PIO (%)
Geographic range size (km^2)
(f)
r^2_{adj} = 0.018
slope = 10.004
Detectability-corrected PIO (%)
Geographic range size (km^2)

1128

Figure S4 Relationships between the proportion of islands occupied (PIO) and species traits included in Phylogenetic Generalised Least Squares (PGLS) models with high support (ΔAIC ≤ 2), namely natural abundance (a and b), habitat breadth (c and d), and geographic range size (e and f). Grey circles represent the 207 bird species surveyed across all 36 islands surveyed at the THR landscape. Observed PIO was quantified as a percentage between the number of islands where a species was recorded divided by the total number of surveyed islands, whereas detectability-corrected PIO was quantified from single-season occupancy models (MacKenzie et al., 2002). See Table S2 for a description of species traits. Note the base 10 logarithmic scales of the *x*-axes in (a), (b), (e) and (f).



1139

1140 **Figure S5** Species-area relationship for birds surveyed across 37 islands at the Thousand
1141 Island Lake in China (data reanalysed from Si et al., 2015) ($P < 0.001$). The dotted line
1142 indicates null predicted numbers of species if forest fragmentation had no effect. Circles,
1143 squares, and triangles correspond to the recorded, extrapolated, and overall number of
1144 species, respectively. Grey region and error bars show the 95% confidence intervals of the
1145 predicted line and the extrapolated value, respectively. See Yu et al. (2012) for an
1146 explanation for the low *z*-value for bird species at the Thousand Island Lake. Note the base 10
1147 logarithmic scales along both axes.

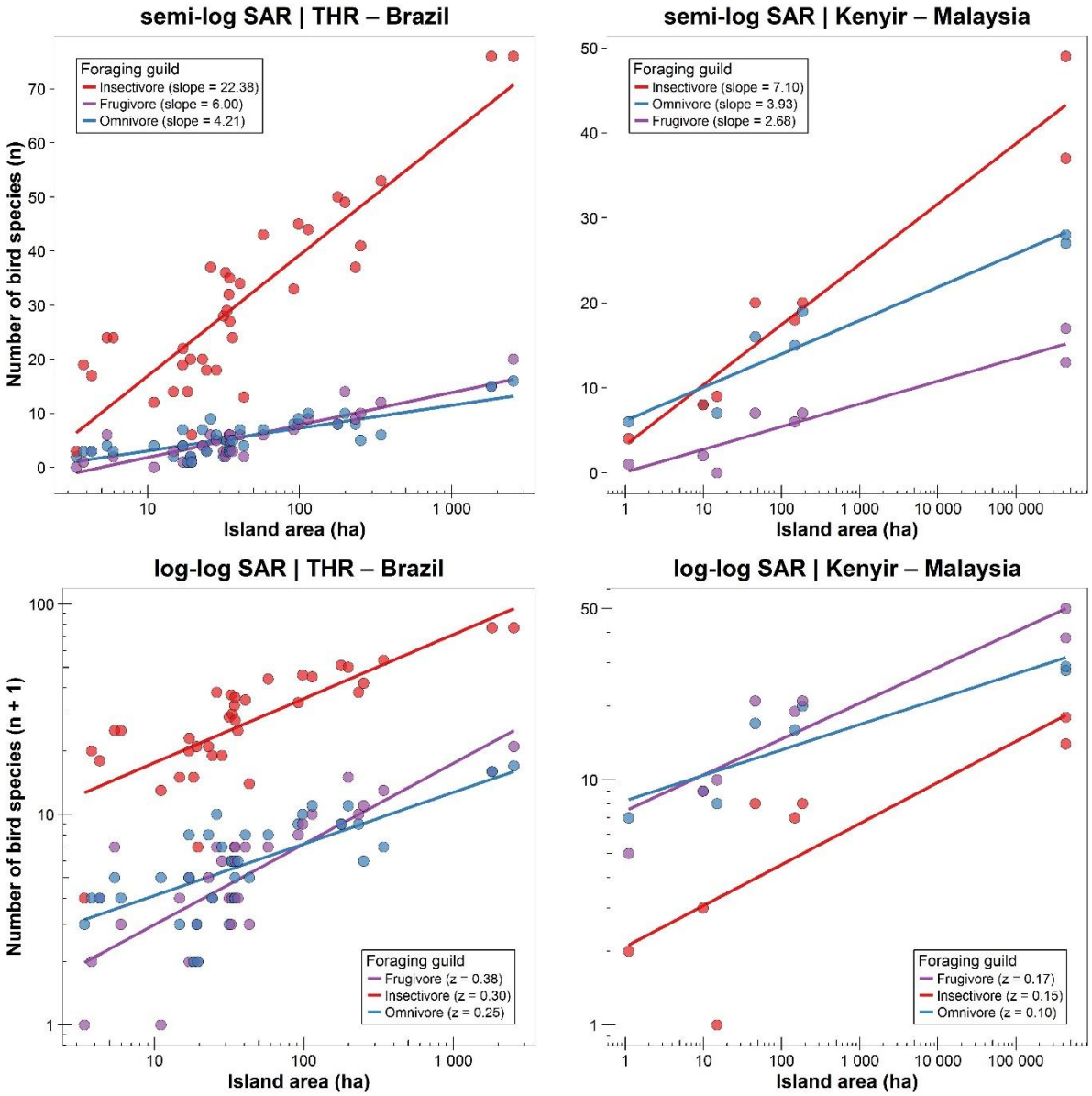
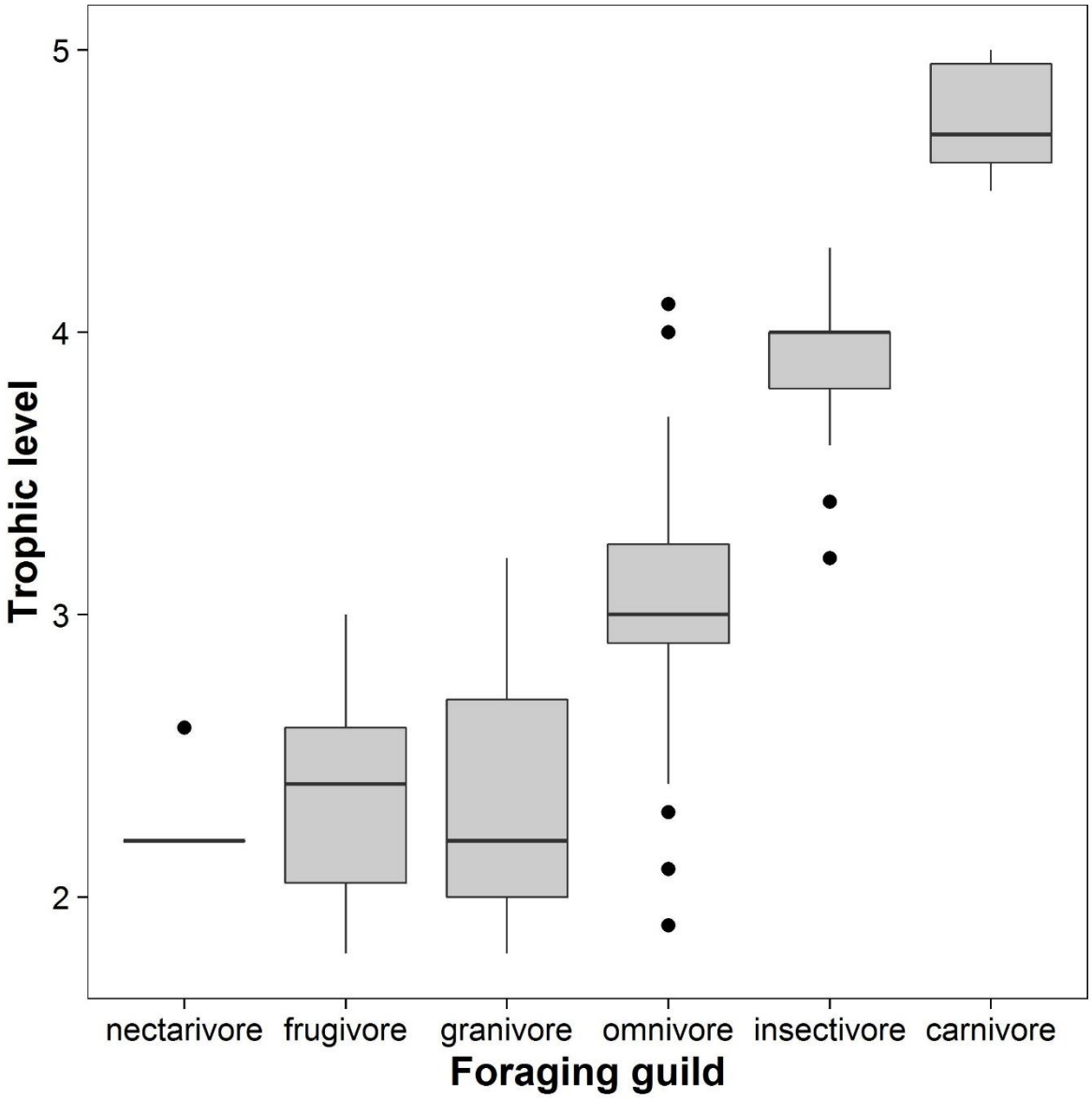


Figure S6 Comparison of the species-area relationships (SARs) for three avian foraging guilds at the THR and Lake Kenyir in Malaysia (data from Yong et al., 2011) ($P \leq 0.01$ in all 12 instances). Plots at the top show the semi-log form of the SARs and their respective slope values, and those at the bottom show the log-log form of the SARs and their respective *z*-values (z). Slope and *z*-values in each plot are sorted by decreasing order, indicating the most (higher values) to the least (lower values) impaired foraging guilds in terms of species losses as a function of island area reduction.



1156

1157 **Figure S7** Distribution of trophic level scores according to avian foraging guild (*sensu*
1158 Wilman et al., 2014) for 207 bird species surveyed across 36 islands at the THR landscape.
1159 Note that the trophic level of some species belonging to a foraging guild may overlap those of
1160 another foraging guild.

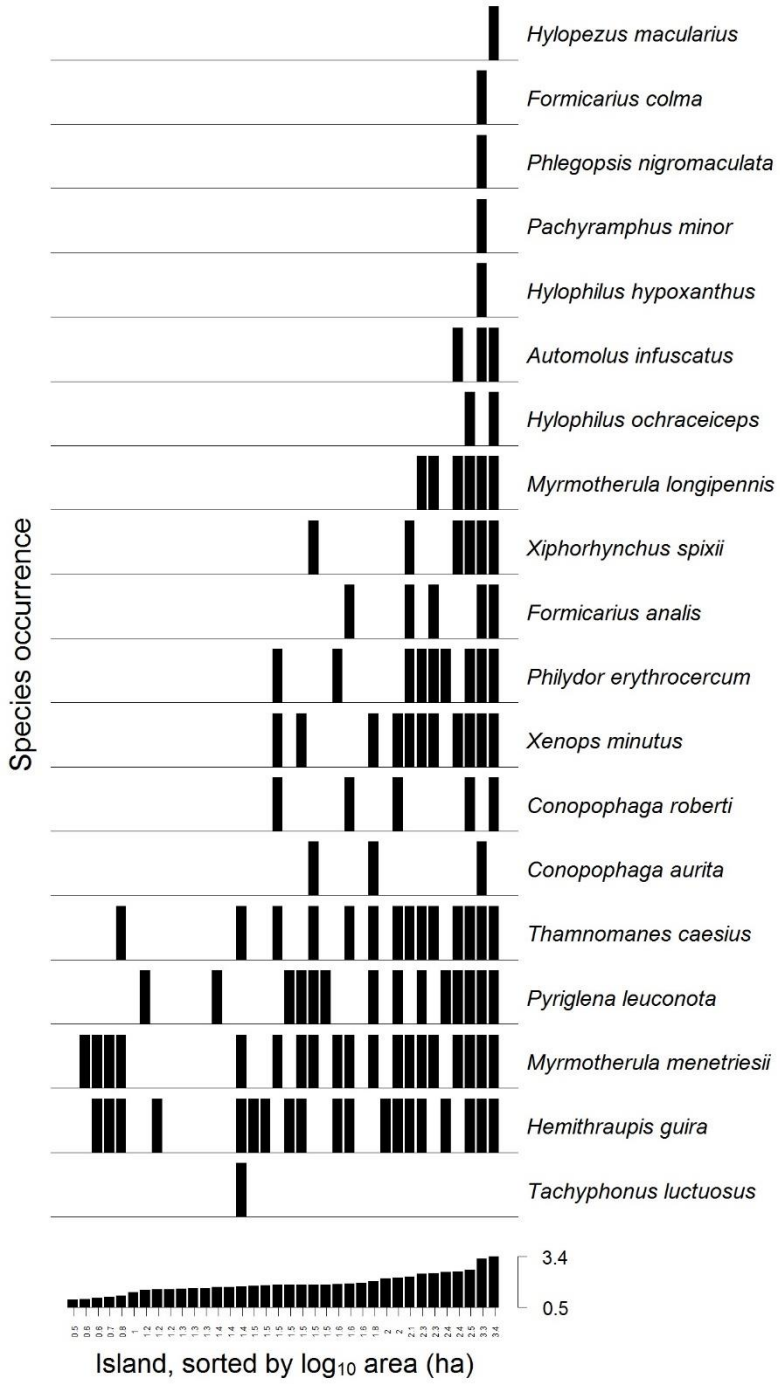


Figure S8 Species occurrence of ground insectivores, obligate ant-followers, and obligate mixed-species flock attendants along the island area gradient. Bars indicate species occurrence on islands, ordered left to right from the smallest to the largest. Bars at the bottom indicate the relative area of each island, which ranged from 3.4 to 2551.5 ha. Ground insectivores: *C. aurita, C. roberti, F. analis, F. colma, H. macularius*; obligate ant-followers: *P. nigromaculata, P. leuconota*; obligate mixed-species flock attendants: *A. infuscatus, H. guira, H. hypoxanthus, H. ochraceiceps, M. longipennis, M. menetriesii, P. minor, P. erythrocercum, T. luctuosus, T. caesius, X. minutus, X. spixii*.

Table S1 Description of the 36 islands surveyed at the THR landscape, and number of bird species occurring therein. 'Effort' indicates the number of point count stations (PCs), and 'Samples' indicates the number of PCs times the number of survey visits per PCs.

Island name	Latitude (S)	Longitude (W)	Area (ha)	Shape index	Proximity index	Effort (PCs)	Samples	S_{fs}[a]	S_{hg}[b]	S_{all}[c]
Divisa	4°12'22"	49°30'04"	2551.45	8.42	40111.28	33	195	49	79	128
Pedral	4°22'44"	49°35'31"	1823.35	5.63	40111.28	21	124	55	64	119
Marcelo	4°09'17"	49°32'45"	342.43	3.97	99.15	13	78	31	45	76
Eduardo	4°18'32"	49°39'17"	251.93	3.59	699.83	13	70	28	35	63
Tamarindo	4°16'09"	49°39'49"	232.74	2.39	1.07	13	78	23	39	62
Prefeito	4°19'51"	49°37'35"	198.66	2.29	813.48	13	76	35	49	84
Cornélio	4°17'15"	49°28'05"	178.27	3.52	64.99	13	78	27	45	72
Bicuda	4°09'30"	49°32'01"	113.99	2.43	4011.13	6	36	27	43	70
Lucyana	4°10'09"	49°33'47"	98.23	2.42	72.43	10	59	23	45	68
Juarez	4°16'29"	49°30'56"	91.55	2.43	9.83	11	65	15	38	53
Miúdo	4°25'15"	49°33'16"	57.75	1.91	1131.61	8	45	23	35	58
Queimada	4°16'23"	49°38'55"	43.09	2.02	450.06	4	19	6	18	24
Nívia-B4	4°14'58"	49°29'41"	40.52	1.91	584.42	4	24	20	33	53
Cornélio-Jr	4°17'42"	49°29'05"	36.18	2.01	86.66	4	20	7	29	36
Chifre	4°17'16"	49°38'04"	34.79	1.80	5.68	4	23	13	29	42
Sidnei	4°20'47"	49°37'32"	34.62	1.54	42.16	4	21	22	25	47
Roca	4°25'41"	49°33'38"	34.35	1.58	18.53	6	36	17	30	47
Gito	4°17'52"	49°36'47"	33.19	2.26	0.42	6	33	9	35	44
Tiago-B4	4°13'52"	49°30'19"	32.53	1.32	1.74	4	23	14	32	46
Urubu-rei	4°16'05"	49°29'25"	31.61	2.70	0.80	3	18	8	30	38
Embaúba	4°18'08"	49°38'12"	28.32	1.97	25.75	4	24	10	21	31
Fantasia	4°15'24"	49°30'07"	26.06	1.51	913.16	4	24	17	37	54
Vandir	4°22'31"	49°33'47"	24.39	1.36	85.16	3	18	8	22	30
Placa	4°19'12"	49°37'51"	22.95	1.56	128.96	4	22	15	23	38
Guariba	4°10'39"	49°32'40"	19.50	1.37	186.97	2	12	2	6	8
Carrapato	4°23'56"	49°34'22"	19.17	1.65	218.36	3	18	13	15	28
Nívia-B3	4°17'38"	49°37'25"	18.30	1.23	9.98	3	15	6	12	18
Lobão	4°18'22"	49°37'38"	17.09	1.89	32.06	4	21	10	19	29
Barranco	4°09'34"	49°34'07"	16.99	1.29	66.34	3	18	8	25	33
Ailton	4°21'06"	49°35'13"	14.74	1.20	2136.92	2	12	7	14	21
Duca	4°17'11"	49°30'25"	11.02	1.44	8.53	3	18	2	18	20
Fora	4°08'26"	49°33'57"	5.95	1.15	20.74	2	12	10	20	30
Panema	4°10'33"	49°33'05"	5.40	1.11	19.78	4	24	13	25	38
Castanha	4°09'03"	49°33'24"	4.29	1.09	52.51	2	8	6	19	25
Chuva	4°10'59"	49°32'29"	3.79	1.09	2200.61	2	12	6	20	26
Caua	4°23'18"	49°34'08"	3.39	1.06	0.01	2	9	0	7	7

[a] S_{fs}: number of forest specialist species

[b] S_{hg}: number of habitat generalist species

[c] S_{all}: overall number of species

1177 **Table S2** Description and sources of seven morpho-ecological traits for bird species
1178 considered in this study.

Ecological trait	Description	Source
Body mass	Species mean body mass (g)	Wilman et al., 2014
Trophic level	Sum of the proportional food consumption in each diet category weighted by an energetic score: (1) foliage and other plant material, (2) fruit and nectar, (3) seed, (4) invertebrate, (5) vertebrate, including carrion. For example, a species relying entirely on invertebrates is assigned a value 4, and a species relying on 50% fruits and 50% invertebrates is assigned a value 3	Wilman et al., 2014
Vertical stratum	Preferred foraging stratum classified into four categories: (1) ground, (2) understorey, (3) midstorey, (4) canopy	Stotz et al., 1996; Henriques et al., 2003; Wilman et al., 2014; personal observation
Flocking behaviour	Degree of gregariousness classified into six categories: (1) solitary or pairs, (2) monospecific flocks, (3) facultative ant-follower, (4) facultative mixed-species flock attendant, (5) obligate ant-follower, and (6) obligate mixed-species flock attendant	Willis & Oniki, 1978; Munn & Terborgh, 1979; Jullien & Thiollay, 1998; Thiollay & Jullien, 1998; Jullien & Clobert, 2000; Willson, 2004; Martínez et al., 2016; personal observation
Geographic range size	Breeding/resident extent of occurrence (km^2)	BirdLife International, 2017
Habitat breadth	Number of habitats used	Stotz et al. 1996
Natural abundance	Total number of individuals recorded within pseudo-control islands	Field surveys

1179

Table S3 Morpho-ecological traits and measures of vulnerability to forest fragmentation for all 207 bird species surveyed across 36 islands at the THR landscape. Taxonomy follows Jetz et al. (2012).

Species, by family	Ecological traits								Measures of vulnerability		Detectability
	Habitat specialisation	Body mass (g)	Trophic Level	Vertical stratum[a]	Flocking behaviour[b]	Geographic range size (km^2)	Habitat breadth[c]	Natural abundance (n)	Observed PIO[d]	Detectability-corrected PIO[e]	
Tinamidae											
Crypturellus cinereus	habitat generalist	506.63	2.0	1	1	6630000	3	2	8.33	8.51	17.50
Crypturellus soui	habitat generalist	216.16	2.4	1	1	15200000	3	0	5.56	22.57	22.40
Crypturellus strigulosus	forest specialist	430.58	2.9	1	1	4650000	1	0	2.78	52.03	25.45
Crypturellus variegatus	forest specialist	378.00	2.0	1	1	9010000	1	1	8.33	16.25	10.08
Tinamus guttatus	forest specialist	686.18	3.0	1	1	5250000	1	0	5.56	53.25	3.77
Tinamus tao	forest specialist	1600.10	2.3	1	1	8520000	2	7	16.67	61.76	5.64
Cracidae											
Crax fasciolata	forest specialist	2600.00	2.0	1	1	4720000	3	0	2.78	67.62	2.74
Mitu tuberosum	forest specialist	2769.46	2.2	1	1	4810000	1	7	16.67	46.12	7.16
Penelope pileata	forest specialist	1249.79	1.8	4	2	1210000	1	8	13.89	48.01	6.66
Pipile cujubi	forest specialist	1195.82	2.3	4	1	2810000	2	0	5.56	46.06	10.75
Accipitridae											
Buteo magnirostris	habitat generalist	269.00	4.6	4	1	23900000	7	0	25.00	59.32	12.25
Buteo nitidus	habitat generalist	519.04	4.8	4	1	15500000	4	2	27.78	65.05	8.57
Buteogallus urubitinga	habitat generalist	1152.87	4.5	1	1	22100000	4	0	2.78	31.66	13.50
Harpagus bidentatus	habitat generalist	215.25	4.2	4	2	17600000	2	0	2.78	32.78	15.04
Columbidae											
Claravis pretiosa	habitat generalist	68.20	3.2	1	1	18900000	4	0	2.78	33.12	3.94
Geotrygon montana	habitat generalist	133.86	2.9	1	1	22600000	3	1	2.78	34.49	9.60
Leptotila rufaxilla	habitat generalist	157.00	3.0	1	1	14300000	4	10	30.56	61.35	10.96
Leptotila verreauxi	habitat generalist	146.88	3.0	1	1	26000000	5	2	22.22	79.04	4.82
Patagioenas speciosa	habitat generalist	258.47	2.0	4	1	16900000	3	1	5.56	7.22	20.19
Patagioenas subvinacea	forest specialist	162.48	2.0	4	1	9170000	3	1	5.56	26.96	5.05
Cuculidae											
Crotophaga ani	habitat generalist	110.09	4.1	2	2	24800000	2	0	2.78	52.13	3.13
Crotophaga major	habitat generalist	148.25	3.5	2	2	15500000	4	0	5.56	58.44	2.14
Piaya cayana	habitat generalist	101.98	4.0	4	1	20200000	5	8	36.11	50.51	21.17
Trochilidae											
Anthracothorax nigricollis	habitat generalist	7.00	2.2	4	1	14900000	4	1	2.78	34.49	9.60
Glaucis hirsutus	habitat generalist	6.76	2.2	2	1	13000000	3	2	25.00	45.84	11.01
Heliothryx auritus	forest specialist	5.40	2.2	4	1	10700000	1	0	2.78	8.41	45.13
Hylocharis sapphirina	habitat generalist	4.40	2.2	2	1	10800000	2	0	2.78	31.84	7.12

Species, by family	Ecological traits								Measures of vulnerability		Detectability
	Habitat specialisation	Body mass (g)	Trophic Level	Vertical stratum[a]	Flocking behaviour[b]	Geographic range size (km^2)	Habitat breadth[c]	Natural abundance (n)	Observed PIO[d]	Detectability-corrected PIO[e]	
Phaethornis ruber	habitat generalist	2.40	2.2	2	1	11300000	3	61	72.22	78.00	48.54
Phaethornis superciliosus	forest specialist	6.30	2.2	2	1	3030000	3	17	8.33	46.95	9.12
Thalurania furcata	habitat generalist	4.19	2.2	2	1	12500000	3	1	2.78	34.49	9.60
Trogonidae											
Trogon melanurus	habitat generalist	114.00	2.6	3	1	8520000	3	2	2.78	45.67	16.64
Trogon rufus	forest specialist	53.80	3.2	3	1	14200000	2	10	16.67	23.69	15.03
Trogon viridis	habitat generalist	89.69	2.9	3	1	11800000	1	26	69.44	83.29	31.36
Momotidae											
Momotus momota	habitat generalist	114.96	3.6	3	1	11300000	6	15	36.11	63.45	15.55
Galbulidae											
Galbula cyanicollis	forest specialist	23.23	4.0	2	1	3350000	1	17	13.89	13.95	49.14
Galbula dea	habitat generalist	27.40	4.0	4	1	6560000	2	13	30.56	33.35	33.32
Jacamerops aureus	forest specialist	62.90	4.1	3	1	8930000	1	1	2.78	9.56	42.30
Bucconidae											
Bucco capensis	habitat generalist	54.00	4.7	3	1	6080000	1	2	5.56	11.24	15.19
Bucco tamatia	habitat generalist	35.50	4.1	3	1	6240000	2	0	5.56	27.23	23.19
Malacoptila rufa	habitat generalist	47.52	4.0	2	1	3660000	1	1	2.78	9.56	42.30
Monasa morphoeus	habitat generalist	87.90	3.9	3	2	10300000	2	2	2.78	9.56	42.30
Monasa nigrifrons	habitat generalist	80.70	4.3	3	2	8880000	4	3	2.78	9.56	42.30
Notharchus hyperrhynchus	habitat generalist	95.89	3.8	4	1	11400000	2	1	5.56	26.96	5.05
Notharchus tectus	habitat generalist	26.80	4.0	4	1	6720000	2	4	38.89	56.24	15.47
Nystalus striolatus	forest specialist	47.00	4.2	4	1	4870000	2	1	5.56	36.26	3.41
Ramphastidae											
Pteroglossus aracari	habitat generalist	250.16	2.4	4	2	6980000	2	10	52.78	85.62	14.42
Pteroglossus bitorquatus	forest specialist	142.00	2.5	4	2	1110000	2	1	13.89	62.67	6.40
Pteroglossus inscriptus	habitat generalist	125.82	2.6	4	2	3920000	3	0	5.56	21.04	33.16
Ramphastos tucanus	habitat generalist	659.58	2.7	4	1	3240000	1	22	58.33	78.29	25.34
Ramphastos vitellinus	forest specialist	360.36	3.0	4	1	5990000	1	13	41.67	78.20	14.98
Picidae											
Campephilus melanoleucos	habitat generalist	256.00	3.6	3	1	13300000	4	12	52.78	92.79	14.60
Campephilus rubricollis	forest specialist	210.71	4.0	3	1	7810000	2	16	44.44	86.83	14.68
Celeus flavus	forest specialist	147.33	3.7	4	1	10300000	3	0	2.78	51.55	1.14
Celeus undatus	forest specialist	64.50	3.8	4	1	2240000	1	1	5.56	32.10	3.55
Colaptes melanochloros	habitat generalist	127.27	3.6	3	1	6390000	3	0	2.78	29.34	3.52
Dryocopus lineatus	habitat generalist	183.19	3.7	4	1	21300000	6	7	55.56	83.83	17.89
Melanerpes cruentatus	forest specialist	58.10	3.0	4	2	7810000	3	2	2.78	22.37	35.31
Piculus chrysochloros	habitat generalist	88.00	4.0	4	1	13300000	3	1	2.78	9.56	42.30
Piculus flavigula	habitat generalist	55.00	4.0	3	4	10300000	2	3	13.89	20.01	11.07

Species, by family	Ecological traits								Measures of vulnerability		Detectability
	Habitat specialisation	Body mass (g)	Trophic Level	Vertical stratum[a]	Flocking behaviour[b]	Geographic range size (km^2)	Habitat breadth[c]	Natural abundance (n)	Observed PIO[d]	Detectability-corrected PIO[e]	
Veniliornis affinis	forest specialist	34.83	3.4	4	4	9290000	2	30	58.33	83.40	24.36
Falconidae											
Daptrius ater	habitat generalist	351.75	4.6	4	2	8090000	3	4	16.67	36.62	8.48
Falco rufigularis	forest specialist	163.64	4.7	4	1	21700000	4	2	16.67	55.41	5.30
Herpetotheres cachinnans	habitat generalist	623.58	5.0	4	1	20400000	5	0	5.56	43.06	35.03
Ibycter americanus	habitat generalist	624.00	4.0	4	2	10700000	2	2	11.11	60.25	3.83
Micrastur mintoni	forest specialist	209.50	4.5	3	1	4110000	1	2	5.56	11.24	15.19
Micrastur ruficollis	habitat generalist	177.64	5.0	3	1	19300000	2	8	25.00	54.73	8.58
Micrastur semitorquatus	habitat generalist	621.68	5.0	4	1	20500000	3	2	5.56	24.56	8.35
Psittacidae											
Amazona amazonica	habitat generalist	370.00	2.0	4	2	12200000	5	4	33.33	70.74	11.03
Amazona farinosa	habitat generalist	625.99	2.1	4	2	11900000	1	11	25.00	47.45	13.77
Amazona ochrocephala	habitat generalist	476.94	2.0	4	2	8010000	4	8	16.67	58.96	5.15
Ara chloropterus	habitat generalist	1214.00	2.0	4	2	10500000	2	8	25.00	64.64	8.56
Ara macao	forest specialist	1015.00	2.0	4	2	10200000	3	0	5.56	74.43	3.37
Ara severus	forest specialist	343.00	2.3	4	2	8470000	4	4	25.00	63.26	13.63
Aratinga leucophthalma	habitat generalist	158.00	2.2	4	2	13200000	4	0	22.22	76.94	5.20
Brotogeris chrysoptera	habitat generalist	54.50	2.3	4	2	3840000	2	34	16.67	23.78	13.79
Deroptyus accipitrinus	forest specialist	246.00	1.8	4	2	5470000	2	3	2.78	34.49	9.60
Guaruba guarouba	forest specialist	194.00	1.8	4	2	516000	1	2	5.56	26.60	5.72
Pionus menstruus	habitat generalist	251.00	2.1	4	2	10100000	4	21	55.56	92.37	15.15
Pyrrhura picta	habitat generalist	62.10	1.9	4	2	392000	2	24	19.44	44.82	8.03
Thamnophilidae											
Cercomacra cinerascens	forest specialist	14.30	4.0	3	1	7420000	1	341	80.56	80.56	86.11
Cercomacra laeta	habitat generalist	15.96	4.0	2	1	1720000	2	54	19.44	19.57	62.70
Cercomacra nigrescens	habitat generalist	16.50	4.0	2	1	6120000	4	2	19.44	20.98	35.83
Cymbilaimus lineatus	habitat generalist	35.80	4.0	3	4	9350000	1	4	5.56	29.76	13.36
Dysithamnus mentalis	habitat generalist	14.87	3.8	2	4	16700000	2	24	30.56	31.46	47.48
Epinecrophylla ornata	forest specialist	9.40	4.0	3	4	1420000	2	17	27.78	31.37	36.98
Formicivora grisea	habitat generalist	10.36	4.0	2	1	8830000	4	9	58.33	60.14	44.67
Herpsilochmus rufimarginatus	habitat generalist	10.58	3.8	4	4	11800000	5	5	27.78	28.47	44.32
Hylophylax naevius	forest specialist	14.20	4.0	2	1	6790000	2	0	5.56	6.60	28.40
Hypocnemis striata	forest specialist	12.29	4.0	2	1	1410000	3	26	38.89	38.91	71.30
Myrmoborus myotherinus	forest specialist	18.80	4.0	2	3	6590000	1	2	8.33	66.39	5.56
Myrmotherula axillaris	forest specialist	8.09	4.0	2	4	10400000	3	166	94.44	94.15	81.37
Myrmotherula brachyura	forest specialist	6.40	4.0	4	4	6790000	3	0	2.78	31.84	7.12
Myrmotherula hauxwelli	forest specialist	10.70	4.1	2	4	5640000	1	30	55.56	57.42	44.79
Myrmotherula longipennis	forest specialist	9.40	4.0	2	6	5930000	1	21	16.67	16.93	37.52

Species, by family	Ecological traits								Measures of vulnerability		Detectability
	Habitat specialisation	Body mass (g)	Trophic Level	Vertical stratum[a]	Flocking behaviour[b]	Geographic range size (km^2)	Habitat breadth[c]	Natural abundance (n)	Observed PIO[d]	Detectability-corrected PIO[e]	
Myrmotherula menetriesii	habitat generalist	8.60	4.0	3	6	6980000	1	35	52.78	55.88	48.59
Phlegopsis nigromaculata	forest specialist	45.24	4.2	2	5	6080000	2	8	2.78	48.62	29.62
Pyriglena leuconota	forest specialist	32.30	4.2	2	5	8450000	3	19	38.89	58.10	19.06
Taraba major	habitat generalist	59.20	4.0	2	1	18300000	5	0	5.56	20.09	8.44
Thamnomanes caesius	forest specialist	15.70	4.0	2	6	9240000	1	134	38.89	39.35	58.56
Thamnophilus aethiops	forest specialist	25.70	4.0	2	4	8180000	1	41	38.89	41.42	46.81
Thamnophilus amazonicus	habitat generalist	18.68	4.0	3	4	7120000	4	5	13.89	20.02	26.34
Thamnophilus palliatus	habitat generalist	23.30	4.0	3	1	7260000	3	7	5.56	5.71	44.22
Thamnophilus schistaceus	forest specialist	20.30	4.0	2	4	5160000	2	26	11.11	19.47	15.82
Thamnophilus stictocephalus	forest specialist	21.50	4.0	2	1	1410000	5	65	44.44	46.61	67.87
Willisornis poecilinotus	forest specialist	18.40	4.1	2	3	738000	1	19	30.56	31.69	41.58
Conopophagidae											
Conopophaga aurita	forest specialist	26.30	4.0	1	1	674000	1	3	8.33	8.63	42.71
Conopophaga roberti	forest specialist	20.80	4.0	1	1	730000	2	20	13.89	14.12	48.90
Formicariidae											
Formicarius analis	forest specialist	62.19	3.9	1	1	10100000	2	9	13.89	14.09	45.10
Formicarius colma	forest specialist	47.00	4.0	1	1	12000000	1	1	2.78	9.56	42.30
Hylopezus macularius	forest specialist	44.20	4.0	1	1	4380000	1	2	2.78	46.21	16.40
Dendrocolaptidae											
Dendrexetastes rufigula	habitat generalist	69.60	3.8	4	1	6340000	2	4	8.33	8.33	16.67
Dendrocincla fuliginosa	habitat generalist	38.70	4.2	2	3	12300000	1	18	75.00	78.88	47.83
Dendrocolaptes certhia	habitat generalist	68.70	4.2	3	3	8970000	1	5	13.89	52.48	7.64
Dendroplex picus	habitat generalist	41.34	4.1	3	4	12500000	5	21	91.67	93.60	47.71
Glyphorynchus spirurus	habitat generalist	14.60	4.0	2	4	13500000	2	26	55.56	58.21	46.60
Hylexetastes brigidai	forest specialist	117.00	4.1	3	3	3310000	1	0	2.78	20.64	26.97
Lepidocolaptes albolineatus	habitat generalist	20.30	4.0	4	4	2390000	1	34	75.00	94.39	39.26
Sittasomus griseicapillus	habitat generalist	13.12	3.7	3	4	13700000	5	11	13.89	49.69	12.07
Xiphorhynchus guttatus	habitat generalist	59.69	4.2	3	4	7680000	1	56	69.44	73.14	46.65
Xiphorhynchus spixii	forest specialist	31.20	4.0	2	6	1110000	1	23	16.67	33.49	11.73
Furnariidae											
Automolus infuscatus	forest specialist	32.90	4.1	2	6	1940000	1	10	8.33	8.33	39.83
Philydor erythrocercum	forest specialist	25.27	4.0	3	6	7100000	2	19	25.00	29.87	20.35
Synallaxis rutilans	forest specialist	16.70	4.0	2	1	6770000	1	7	22.22	25.47	23.86
Xenops minutus	forest specialist	10.60	4.0	3	6	14000000	2	14	30.56	36.49	26.17
Tyrannidae											
Attila cinnamomeus	habitat generalist	38.80	3.7	3	1	6400000	1	5	2.78	48.55	24.35
Attila spadiceus	habitat generalist	39.10	4.0	3	1	18100000	3	21	44.44	80.89	16.74
Camptostoma obsoletum	habitat generalist	8.10	3.4	4	1	17900000	6	8	72.22	73.94	47.26

Species, by family	Ecological traits								Measures of vulnerability		Detectability
	Habitat specialisation	Body mass (g)	Trophic Level	Vertical stratum[a]	Flocking behaviour[b]	Geographic range size (km^2)	Habitat breadth[c]	Natural abundance (n)	Observed PIO[d]	Detectability-corrected PIO[e]	
Cnemotriccus fuscatus	habitat generalist	13.60	4.0	2	1	14300000	6	0	11.11	64.88	8.36
Empidonomus varius	habitat generalist	27.10	3.2	4	1	12900000	4	0	2.78	52.03	25.45
Hemitriccus griseipectus	forest specialist	8.90	4.0	3	1	5220000	2	5	8.33	22.74	8.25
Hemitriccus minor	forest specialist	7.40	4.0	3	1	2920000	1	16	38.89	39.04	71.02
Inezia subflava	habitat generalist	8.40	4.0	2	1	4130000	3	0	2.78	54.70	6.33
Lathrotriccus euleri	habitat generalist	11.33	4.0	2	1	15000000	3	1	2.78	34.49	9.60
Legatus leucophaius	habitat generalist	22.20	2.6	4	1	18600000	4	2	13.89	26.79	8.62
Lophotriccus galeatus	habitat generalist	6.60	4.0	3	1	4780000	2	73	50.00	50.00	87.15
Megarynchus pitangua	habitat generalist	69.91	3.8	4	1	20500000	5	1	2.78	9.56	42.30
Mionectes oleagineus	habitat generalist	11.17	2.4	2	4	16600000	3	1	11.11	27.31	6.77
Myiarchus ferox	habitat generalist	27.50	3.0	3	1	13600000	4	19	80.56	89.05	38.32
Myiarchus tuberculifer	habitat generalist	17.70	3.7	4	1	22400000	5	15	52.78	56.24	34.71
Myiodynastes maculatus	habitat generalist	43.20	3.7	4	1	9770000	4	3	38.89	69.82	12.39
Myiopagis caniceps	forest specialist	10.50	3.6	4	4	6650000	1	0	2.78	80.13	20.37
Myiopagis gaimardii	forest specialist	12.02	3.6	4	4	12100000	3	46	91.67	96.37	58.68
Myiornis ecaudatus	habitat generalist	5.25	4.0	3	4	7600000	2	20	50.00	50.38	54.55
Onychorhynchus coronatus	habitat generalist	14.00	4.0	3	4	7160000	1	8	11.11	33.97	8.28
Ornithion inerme	habitat generalist	7.00	4.0	4	4	10200000	2	18	27.78	34.30	23.77
Pitangus lictor	habitat generalist	25.50	4.0	2	1	12400000	2	1	13.89	68.06	3.37
Pitangus sulphuratus	habitat generalist	62.85	3.7	4	1	28600000	5	2	30.56	43.63	18.11
Platyrinchus platyrhynchos	forest specialist	12.00	4.0	3	1	6410000	1	1	5.56	8.38	34.93
Poecilotriccus sylvia	habitat generalist	7.10	4.0	2	1	7120000	5	38	27.78	30.90	36.11
Rhynchocyclus olivaceus	forest specialist	21.30	4.0	2	4	6050000	2	10	25.00	29.12	23.55
Rhytipterna simplex	forest specialist	31.80	3.6	3	1	11300000	1	13	19.44	22.90	26.96
Todirostrum chrysocrotaphum	habitat generalist	7.00	4.0	4	1	5860000	3	10	11.11	73.19	4.30
Tolmomyias flaviventris	habitat generalist	12.20	3.6	3	4	10200000	5	33	86.11	87.24	53.08
Tolmomyias poliocephalus	habitat generalist	10.80	4.0	4	4	10000000	3	47	55.56	57.28	48.39
Tolmomyias sulphurescens	habitat generalist	14.30	3.8	3	1	19200000	6	41	50.00	50.56	53.91
Tyrannulus elatus	habitat generalist	7.00	3.2	4	1	8700000	4	13	27.78	31.10	27.99
Tyrannus melancholicus	habitat generalist	37.40	4.0	4	1	28500000	5	0	16.67	75.15	20.09
Zimmerius acer	forest specialist	7.13	3.4	4	1	2730000	2	24	52.78	55.02	44.27
Cotingidae											
Gymnoderus foetidus	forest specialist	275.49	2.4	4	1	7480000	2	0	2.78	8.41	45.13
Lipaugus vociferans	forest specialist	75.42	3.0	3	1	10600000	1	29	33.33	33.93	42.62
Pachyramphus castaneus	habitat generalist	19.50	3.8	4	1	11500000	4	8	25.00	43.35	12.50
Pachyramphus marginatus	forest specialist	18.40	3.0	4	4	11000000	1	5	27.78	36.26	20.38
Pachyramphus minor	forest specialist	36.60	3.0	4	6	7380000	1	1	2.78	9.56	42.30
Querula purpurata	forest specialist	107.35	3.0	4	2	8790000	1	4	5.56	5.56	16.70

Species, by family	Ecological traits								Measures of vulnerability		Detectability
	Habitat specialisation	Body mass (g)	Trophic Level	Vertical stratum[a]	Flocking behaviour[b]	Geographic range size (km^2)	Habitat breadth[c]	Natural abundance (n)	Observed PIO[d]	Detectability-corrected PIO[e]	
Schiffornis turdina	forest specialist	31.70	3.0	2	1	10400000	2	8	11.11	11.10	62.52
Tityra inquisitor	habitat generalist	43.10	2.4	4	1	18100000	2	4	5.56	8.51	10.83
Pipridae											
Lepidothrix iris	forest specialist	8.00	2.4	2	1	983000	1	0	2.78	8.41	45.13
Pipra fasciicauda	forest specialist	15.90	2.2	2	1	7620000	4	45	33.33	36.58	32.65
Pipra	forest specialist	11.11	2.8	2	1	11300000	2	5	8.33	30.93	4.65
Pipra rubrocapilla	forest specialist	12.00	2.4	2	1	7060000	1	7	8.33	8.36	46.72
Piprites chloris	forest specialist	16.00	3.8	4	4	12900000	2	3	5.56	6.85	26.35
Tyranneutes stolzmanni	forest specialist	7.20	2.4	3	1	6540000	1	5	33.33	42.78	25.41
Vireonidae											
Cyclarhis gujanensis	habitat generalist	28.80	4.0	3	1	21700000	4	13	30.56	31.43	45.60
Hylophilus hypoxanthus	forest specialist	17.00	4.0	4	6	4980000	1	3	2.78	48.62	24.32
Hylophilus ochraceiceps	habitat generalist	11.60	3.6	2	6	10600000	1	1	5.56	8.51	10.83
Hylophilus semicinereus	habitat generalist	13.00	4.0	3	4	5270000	3	3	11.11	17.10	15.91
Vireo olivaceus	forest specialist	16.06	3.4	4	1	52900000	5	1	8.33	15.29	10.17
Troglodytidae											
Campylorhynchus turdinus	forest specialist	32.60	3.6	4	1	9110000	4	39	55.56	55.82	61.26
Microcerculus marginatus	forest specialist	18.22	4.0	2	1	8480000	1	4	2.78	48.54	24.35
Thryothorus coraya	habitat generalist	17.20	3.8	2	1	5500000	3	24	30.56	30.63	63.48
Thryothorus genibarbis	habitat generalist	19.20	4.0	2	1	8790000	5	213	41.67	41.70	74.56
Troglodytes aedon	habitat generalist	10.85	3.4	2	1	59200000	5	10	83.33	91.62	40.47
Polioptilidae											
Polioptila plumbea	habitat generalist	6.00	4.0	4	4	15800000	6	0	2.78	14.81	8.91
Ramphocaenus melanurus	forest specialist	9.70	4.0	3	4	16400000	2	59	36.11	37.60	42.37
Turdidae											
Turdus albicollis	habitat generalist	54.00	3.2	3	1	15100000	1	1	2.78	9.56	42.30
Thraupidae											
Cissopis leverianus	habitat generalist	76.00	2.6	4	2	11000000	3	0	2.78	31.84	7.12
Conirostrum speciosum	habitat generalist	8.80	3.4	4	1	13100000	4	0	22.22	30.15	20.30
Dacnis cayana	habitat generalist	13.00	2.9	4	4	15700000	4	0	2.78	32.78	15.04
Euphonia violacea	habitat generalist	15.00	2.0	3	4	9350000	3	0	5.56	20.64	5.39
Hemithraupis guira	habitat generalist	12.00	3.7	4	6	14300000	3	27	52.78	57.28	35.49
Lamprospiza melanoleuca	forest specialist	34.00	2.9	4	2	4670000	1	3	11.11	13.37	13.89
Ramphocelus carbo	habitat generalist	25.92	3.0	2	2	11500000	5	40	91.67	91.77	65.40
Tachyphonus luctuosus	habitat generalist	13.00	3.6	3	6	10700000	3	0	2.78	24.68	15.72
Tangara mexicana	habitat generalist	20.50	3.0	4	2	7710000	5	0	2.78	62.48	2.42
Thraupis episcopus	habitat generalist	35.00	2.7	4	2	13300000	4	0	5.56	43.96	32.54
Thraupis palmarum	habitat generalist	39.00	2.4	4	4	15300000	6	2	16.67	59.50	4.77

Species, by family	Ecological traits								Measures of vulnerability		Detectability
	Habitat specialisation	Body mass (g)	Trophic Level	Vertical stratum[a]	Flocking behaviour[b]	Geographic range size (km^2)	Habitat breadth[c]	Natural abundance (n)	Observed PIO[d]	Detectability-corrected PIO[e]	
Coerebidae											
Coereba flaveola	habitat generalist	10.01	2.6	4	4	22400000	5	1	27.78	89.57	5.76
Emberizidae											
Arremon taciturnus	forest specialist	24.80	2.9	1	1	9910000	1	27	44.44	46.70	43.34
Oryzoborus angolensis	habitat generalist	13.00	2.4	2	1	13900000	3	0	2.78	24.06	4.06
Cardinalidae											
Cyanocompsa cyanoides	habitat generalist	32.50	2.5	2	1	7600000	2	5	5.56	29.40	4.24
Granatellus pelzelni	habitat generalist	11.20	4.0	3	4	693000	1	8	19.44	28.23	13.89
Saltator grossus	habitat generalist	44.20	3.2	3	1	9340000	1	13	8.33	9.87	40.32
Saltator maximus	habitat generalist	47.62	3.2	3	1	15400000	3	1	11.11	66.62	2.96
Icteridae											
Cacicus cela	habitat generalist	85.45	2.8	4	2	11200000	4	2	11.11	24.82	9.36
Icterus cayanensis	habitat generalist	35.44	3.4	4	2	5290000	3	0	11.11	46.44	6.37
Psarocolius bifasciatus	forest specialist	335.70	3.0	4	2	178000	3	0	2.78	80.13	20.37
Psarocolius decumanus	habitat generalist	206.30	2.8	4	2	13900000	3	0	11.11	74.69	2.68

[a]Vertical stratum: (1) ground, (2) understorey, (3) midstorey, (4) canopy.

[b]Flocking behaviour: (1) solitary or pairs, (2) monospecific flocks, (3) facultative ant-follower, (4) facultative mixed-species flock attendant, (5) obligate ant-follower, (6) obligate mixed-species flock attendant.

[c]Habitat breadth: number of habitats used.

[d]Observed PIO: proportion of islands occupied not corrected for imperfect detectability.

[e]Detectability-corrected PIO: proportion of islands occupied corrected for imperfect detectability.

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